

THE PANORPOID COMPLEX.

PART 3:—THE WING-VENATION.

By R. J. TILLYARD, M.A., D.Sc., F.L.S., F.E.S., LINNEAN
MACLEAY FELLOW IN ZOOLOGY.

(Plates xxxi.—xxxv. and Text-figures 35-112.)

CONTENTS.

| | | |
|---------------|---|-----|
| INTRODUCTION | ... | 536 |
| Section i. | —THE BASAL TRACHEATION OF THE PUPAL WING | 542 |
| Section ii. | —THE MAIN VEINS AND THEIR BRANCHES | 547 |
| | The Costa and Subcosta | 548 |
| | The Radius and Radial Sector | 550 |
| | The Media | 552 |
| | The Cubitus | 553 |
| | The Anal Veins | 554 |
| Section iii. | —THE ARCULUS AND CUBITO-MEDIAN Y-VEIN | 554 |
| | Its formation in the Paramecoptera | 557 |
| | " " " Mecoptera | 560 |
| | " " " Trichoptera | 561 |
| | " " " Lepidoptera | 562 |
| | " " " Diptera | 565 |
| | " " " Megaloptera | 566 |
| | " " " Planipennia | 567 |
| Section iv. | —THE STRUCTURE OF THE CUBITUS | 570 |
| Section v. | —THE ANAL VEINS | 576 |
| | The Cubito-Anal Y-vein | 577 |
| | The Anal Y-vein | 578 |
| Section vi. | —THE DISTAL Y-VEIN, TRIGAMMA, BASAL CELL AND AREOLE IN THE LEPIDOPTERA | 584 |
| | The Distal Y-vein | 585 |
| | The Trigamma | 590 |
| | The Basal Cell and Areole | 590 |
| Section vii. | —VEINLETS AND CROSS-VEINS | 592 |
| Section viii. | —THE VENATION OF THE MECOPTERA | 596 |
| | The Venation of the genus <i>Merope</i> | 599 |
| | Table of the Principal Venational Characters for the Families | 603 |
| Section ix. | —THE VENATION OF THE PARAMECOPTERA | 605 |
| Section x. | —THE VENATION OF THE PROTOMECOPTERA | 607 |
| | Comparison with the Paramecoptera | 609 |
| Section xi. | —THE VENATION OF THE PARATRICHOPTERA | 611 |
| | Comparison with the Mecoptera | 613 |
| Section xii. | —THE VENATION OF THE DIPTERA | 614 |
| | Comparison with the Paratrachoptera | 620 |
| | Venation of freshly-emerged imagines | 621 |
| | Internal Phylogeny of the Order | 623 |
| Section xiii. | —THE VENATION OF THE TRICHOPTERA | 624 |
| | Lines of specialisation within the Order | 629 |

| | |
|--|-----|
| Section xiv. —THE VENATION OF THE LEPIDOPTERA | 631 |
| The Archetype of the Order | 631 |
| Relationship with the Trichoptera | 634 |
| Venational Studies:— | |
| Suborder HOMONEURA | 636 |
| Division Jugo-frenata | 636 |
| „ Jugata | 639 |
| Fam. Hepialidae | 639 |
| „ Prototheoridae | 647 |
| Table of the Principal Venational Characters for the Families of the Homoneura | 650 |
| Note on the Evidence concerning the Existence of Vein M ₄ in the Lepidoptera | 651 |
| Suborder HETERONEURA | 653 |
| Fam. <i>Palacontinidae</i> (fossil) | 654 |
| Fam. <i>Cossidae</i> | 658 |
| Superfam. Tortricina | 664 |
| Superfam. Tineina | 666 |
| Fam. <i>Castniidae</i> | 672 |
| Superfam. Psychina | 674 |
| „ Pyralidina | 677 |
| The Butterflies, or Superfam. Rhopalocera | 679 |
| The Archetype of the Heteroneura .. | 687 |
| Table of the Principal Venational Characters for the more archaic groups of the Heteroneura, and the Butterflies.. | 690 |
| Section xv. —THE VENATION OF THE MEGALOPTERA | 691 |
| Section xvi. —THE VENATION OF THE PLANIPENNIA | 699 |
| Comparison with the Megaloptera | 703 |
| Section xvii. —PHYLOGENETIC RESULTS | 703 |
| The Venation of the Archetype of the Panorpoïd Complex | 704 |
| Table of the Characters of the Wings for the Archetypes of the Complex and its Orders | 705 |
| The Phylogeny of the Orders of the Complex | 706 |
| Phylogenetic Diagram | 709 |
| Appendix A.—NOTE ON THE WING-COUPPLING APPARATUS OF THE JUGO-FRENATA | 712 |
| Appendix B.—NOTE ON THE OCCURRENCE OF THE RETINACULA IN THE LEPIDOPTERA HETERONEURA | 712 |
| Appendix C.—NOTE ON THE RESTING-POSITION OF THE WINGS IN THE PANORPOID COMPLEX | 714 |
| BIBLIOGRAPHY | 715 |
| EXPLANATION OF PLATES | 717 |

LETTERING OF PLATES AND TEXT-FIGURES.

A, anal veins; 1A, 2A, 3A, first, second and third anals; 1A-2A, fused first and second anals, forming a Y-vein; *act*, areocel; *af*, anal furrow; Af₁, Af₂, Af₃, Af₄, Af₅, the five apical forks in Trichoptera; *arc*, arculus; *bc*, basal cell in Lepidoptera; C, costal trachea or vein; Cu, cubitus; Cu₁, Cu₂, its two primary branches, separating at *cuf*, the primary cubital fork; Cu_{1a}, Cu_{1b}, the secondary branches of Cu₁, separating at *cuf'*, the secondary cubital fork; Cu₂-1A, fused second cubitus and first analis, forming an incomplete Y-vein; *Cul*, cubital trachea, in Text-fig. 92; *cu-a*, cubito-anal cross-vein (but not in Text-fig. 37); *dco*, distal costal veinlet; *fr*, frenulum; *hm*, humeral cross-vein; *ia*₁, *ia*₂, first and second inter-anal cross-vein; *icu*, inter-cubital cross-vein; *icv*, intermediate costal veinlet; *im*, intermedian cross-vein; *ir*, inter-radial cross-vein closing radial cell; *ir'*, upper inter-radial cross-vein, between R₁ and R₂; *jb*, jugal bristles; *yg*, jugum; *jl*, jugal lobe; M, media; M₁₋₄, M₅, its primary branches, separating at *mf*, the primary median fork; M₁₋₂, M₃₋₄, the secondary branches of M₁₋₄, separating at *mf'*, the secondary median fork; M₁, M₂, M₃, M₄, branches of M₁₋₄ (further branches are indicated by using the suffixes *a*, *b*,); M₄ — Cu_{1a}, the fused stem of the distal Y-vein in Lepidoptera; M₅ — Cu₁, the fused stem of the cubito-median Y-vein; Mt, median trachea in Text-fig. 92; *m-cu*, medio-cubital cross-vein; *mc*, median cell, closed distally by cross-vein *im*; *pt*, pterostigma; *ptf*, pterostigmatic furrow; R, radius; R₁, R_s, its primary branches, separating at *rf*, the primary radial fork; R_{1a}, R_{1b}, distal branches of R₁; R₂₋₃, R₄₋₅, secondary branches of R_s, separating at *rf'*, the secondary radial fork; R₂, R₃, R₄, R₅, branches of R_s, (further branches are indicated by using the suffixes *a*, *b*,); *r-m*, radio-median cross-vein; *rc*, radial cell (areole in Lepidoptera), closed distally by cross-vein *ir*; *rt*, subcostal retinaculum; *rt'*, subdorsal retinaculum; *sa*, subanal cross-vein; Sc, subcosta; Sc', its upper basal branch; Sc₁, Sc₂, its distal branches; Sc-R, fused subcosta and radius in Text-fig. 43; Sc-R₁, fused subcosta and first radius; *sc-r*, subcosto-radial cross-vein; *sh*, subhumeral cross-vein; *sm*, submedian cross-vein; *sp*, wingspot in Trichoptera, between R₄ and R₅; *x*, true cross-vein in Text-fig. 57, (without macrotrichia).

INTRODUCTION.

(Text-fig. 35.)

The study of the Wing-Venations of the Orders comprising the Panorpoïd Complex has proved a difficult and protracted task; and the results, even with the greatest possible amount of condensation, will occupy quite as much space as can be fairly allotted to a single part of this work. That being so, I have decided to dispense with the usual introductory remarks upon the general scheme of wing-venation, and to embark upon the details of the actual research with the briefest possible indication of the premises on which they are founded. For those who have not yet mastered the Comstock-Needham system, either the earlier work of these authors (14*), or the excellent later book by Comstock (15), will be found to contain all that is necessary for the complete understanding of the venational notation; while Text-fig. 37 reproduces Comstock's original diagram showing this notation applied to his hypothetical venational type.

As a basis for my study, I have not been content to accept merely the reference to the precedent pupal tracheation, valuable as it is. It must be recalled that, in three of the Orders with which we have to deal, this pupal tracheation is greatly reduced, and of little value in the determination of homologies. Moreover, since Part 2 was written, two new fossil Orders belonging to the Complex have come to light (28, 29); so that, besides the three recent Orders just mentioned, there are also three fossil Orders, now extinct, to which this method is not applicable. We may put the position thus:—

(1) *Orders only known as fossils*:—Protomecoptera, Paramecoptera, Paratrachoptera.

(2) *Recent Orders with reduced pupal tracheation*:—Mecoptera, Trichoptera, Diptera.

(3) *Recent Orders with complete pupal tracheation*:—Megaloptera, Planipennia, Lepidoptera.

The presence of the complete pupal tracheation is an archaic character; so that the last three Orders named must be regarded as more archaic than the three in (2), for the character mentioned. It will be at once obvious that no Order in (2) can be ancestral to any one of the Orders in (3). Those wings, in which the pupal tracheation remains complete, I propose to term *holotracheate*; those in which it is reduced, *merotracheate*.

*The numbers in brackets refer to the Bibliography at the end of the paper.

Comstock and Needham applied the test of the pupal or nymphal tracheation to those Orders in which the wings were holotracheate. In the case of merotracheate types, they were content to obtain results simply by comparative studies of the imaginal wing-venations. Consequently, excellent as is that part of their work which is based upon tracheational studies, their results in the Orders placed in (2) above, as well as in the Hymenoptera, do not carry the same conviction, and errors have unfortunately crept in which might have been avoided by more complete methods.

After having spent a very large amount of time, during the past three years, upon this research, I have found the following methods yield good results —

(A) *Study of the Pupal Tracheation.* This is the essential basis of the study of the wing-venation in the Megaloptera, Planipennia and Lepidoptera. But I soon found, in the course of my researches, that not enough attention had been paid to the age of the pupa studied. In the Megaloptera and Planipennia, unless the pupa is taken fairly early, the wing becomes folded in its sheath, and the courses of the tracheæ cannot be followed at all. But, in the Lepidoptera, the wings of older pupæ can be withdrawn from their sheaths without damage to the tracheation. Thus it frequently happens that results in this Order have been obtained from a study of advanced pupæ; yet nobody, so far as I know, has noticed that the tracheation in the advanced pupa may differ very materially from that of the freshly-turned pupa, and may lead to erroneous conclusions. The rule which I followed, and which seems to have only one exception, was this:—*Study the pupal tracheation as soon after the formation of the pupa as possible; in any case, remember that it is the freshly-turned pupa that exhibits the most archaic arrangement of the tracheæ, while older pupæ very often show specialisations towards the type of tracheation preserved in the imago.* The exception to be noted is, that, sometimes, in the case of a fusion of veins, *both* the tracheæ underlying the two fused veins do not develop in the pupa, but only one; and that one, as a rule, is *the trachea which underlies the more convex of the two veins in question.* The other trachea, however, frequently develops late in pupal life, or is to be found in the fused vein of the imago directly after metamorphosis; so that the double nature of the vein is indicated by its carrying two tracheæ.

The variations in the tracheation of the wings of Lepidoptera during pupal life appear to me to be of such importance that I have paid special attention to them in dealing with the venation of this Order in Section xiv.

In the case of wings of merotracheate type, the pupa should always be examined, when obtainable; for some evidence of value may be gained in this way. Moreover, such wings may also show a progressive change in their venational scheme, as the pupa ages, and these changes must be noted.

(B) *Study of the Wing-Trichiation.* The distribution of the macrotrichia upon the wing-veins in the Panorpoid Complex is of the greatest value in determining homologies in difficult cases. The rule, which I have already proved much more fully in Part 2 of this work (25) may be briefly stated as follows:—*In the more archaic types of every Order within the Complex, the main veins and their branches carry macrotrichia, while the cross-veins do not.* The specialised groups, in which the cross-veins, as well as the main veins, carry macrotrichia, are the Raphidioidea, and the higher families of the Planipennia. These will scarcely be needed at all in our search for the Archetypic Venational Schemes of the separate Orders.

latter case, there are many examples of the retention of the base of the wing, in a number of types, where the chitinisation of the basal parts of certain veins, particularly M and Cu, may be so weakened as not to carry macrotrichia; or (b) where the basal portion of the weaker (more concave) of two veins taking part in a fusion becomes more or less transverse in direction, and begins to take on the character of a cross-vein. But, even in this latter case, there are many examples of the retention of the macrotrichia.

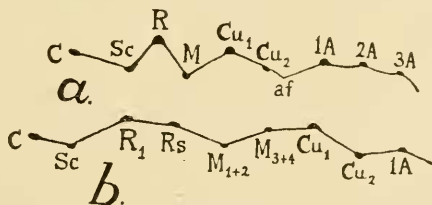
It should also be borne in mind that true cross-veins are not preceded by tracheæ. A main vein, or part, of it, may occasionally lose its trachea; but true cross-veins never possess tracheæ in the freshly-turned pupal wing, though they may sometimes gain them as special outgrowths from the main tracheæ, either later in pupal life, or at metamorphosis.

(C) *The Palaeontological Evidence.* This is of the utmost importance, but needs to be used with great care. The tracheation test cannot be used in the case of fossils; but it frequently happens that the sockets of the macrotrichia are preserved, and their presence or absence may decide a point of great value.

Fossil types must be carefully compared with recent types showing closely similar venations; but wide generalisations, based for the most part upon the study of many types lying outside the bounds of the Complex, must be avoided, as tending to give very misleading results. As an example of this, we may cite Comstock's insistence on a single primitive venational type (15 Chap. iv.), which he constructed largely with the aid of the Carboniferous Palæodictyoptera, and then applied to the Lepidoptera and other Orders within the Panorpid Complex. The primitive type to be considered in this paper will not be the one constructed by Comstock, but one constructed on the evidence obtainable *within the Complex only*; and it will be found to differ in certain very important respects from that type which, whether it was the primitive type for the Pterygote Insects or not, was certainly not, in some of its essential characters, the primitive type from which the Panorpid Orders were derived.

As an instance of the value of the palæontological data, let anyone after reading this paper, cut right out of it all the evidence afforded by the three fossil Orders Protomecoptera, Paramecoptera and Paratrichoptera, and then consider what chance there would have been of a correct conclusion on the remaining evidence alone! Let him also consider what the result might have been, if not only this evidence, but also that afforded by the fossil representatives of still existing Orders, had not been available? It is not always difficult to construct a simple theory that will fit all the known facts; the chances that Nature, in the course of Evolution, followed the direct path that such a theory is sure to lay down, are actually very small indeed.

(D) *Convex and Concave Veins*. It is easy to demonstrate that the more archaic types within every Order of the Panorpid Complex show the same arrangement of Convex and Concave



Text-fig.35.

Two sections across a wing of Panorpid type, to show alternation of convex and concave veins. *a*, close to base; *b*, beyond *rf* and *mf'*. Lettering as on p.535. (Cf. Text-fig-16, corrected, on p.713).

Veins. Text-fig. 35 shows, diagrammatically, the condition of the veins when viewed by a cut taken somewhat obliquely across the wing, (*a*) not far from the base, so as to include only the main stems of the main veins, and (*b*) beyond the first forkings of R and M_{1-4} . Rs, like R_1 , is convex near its origin. Further distad, there is a tendency for the branches of M and R to arrange themselves at very much the same levels on a plane surface, so that the part of the wing lying between the two very strongly convex veins R_1 and Cu_1 is often nearly flat. However, in many types, it can be seen that there are actual differences of level, as in Text-fig. 35 *b*, right to the apex of the wing.

The general rule for the insect wing is that *concave and convex veins follow one another alternately*. Consequently, if two convex veins are seen next to one another, a strong presumption arises that a concave vein has become suppressed between them. Thus, for example, in the higher Lepidoptera, two very strong convex veins (Rs and Cu_1) form the anterior and posterior borders of the closed *basal cell*. This fact should at once suggest that the concave vein M has been suppressed between them; and an examination of the pupal tracheation proves this to be the case.

A more difficult problem, of which no solution has been attempted before, lies in the fact that, in the Panorpoïd type of wing, veins M_{3+4} and Cu_1 are both convex, yet lie next to one another. There is thus a strong antecedent probability that a missing branch of M, viz. M_5 has been suppressed between them. The working out of this problem is shown in this paper, and offers a very interesting example of how the four types of evidence here arranged under the headings A to D may be used together, to furnish a satisfactory proof, which could not be supplied by anything less than all four of them.

There is also the question of the anal veins, which, as shown in Text-fig. 35 *a*, are all convex, though sometimes separated by depressions or furrows. The suggestion that they may be, after all, only so many branches of a single convex vein, as in the Odonata, is worth consideration, and has been studied in this paper, in the light of the evidence afforded by the pupal tracheation.

(E) *Atavisms, or Reversions to Type*. It sometimes happens that a single individual of a species, here and there, reproduces a more archaic condition in its venation than is usual for the

species. This is an *atavism*, or reversion to type. All such occurrences need to be carefully noted; and the changes that occur should be carefully compared with known archaic conditions. Comstock (15) has recorded quite a number of instances of this in the Planipennia and Megaloptera, particularly with respect to the retention of the primitive dichotomic forking of R_{4+5} . In the Lepidoptera, the family *Hepialidae* is occasionally subject to atavisms, which are of special interest, owing to the very archaic position of this family within the Order at the present day. Thus Comstock (15, fig. 335) has recorded a specimen of *Pielus labyrinthicus*, in the forewing of which R_5 is itself forked, and I have myself seen a specimen with a very similar forking. We know from the venation of *Belmontia* (Text-fig. 63) that the Permian Paramecoptera had this vein forked. Thus the atavism serves to strengthen our belief that the *Hepialidae* are descended from ancestors which possessed the Paramecopterous forking of R_5 . Comstock (15, fig. 337) also mentions the famous specimen of *Sthenopsis*, in which the hindwing had M_4 and Cu_{1a} only partially fused. This is the same condition which we find in the Triassic fossil *Archipanorpa*; and there can be no doubt that the ancestors of the Lepidoptera must at one time have passed through a stage in which the two originally separate veins M_4 and Cu_{1a} were only partially fused, as in this atavistic individual of *Sthenopsis*.

As it is impossible to say definitely that the condition shown in an atavistic individual actually belonged to the Order in question, seeing that it may just as well be an atavistic reproduction of a character preserved in the ancestral Order only, and not in the Order descended from it, to which the specimen now belongs, I have not admitted the evidence of these atavisms as sufficient, *per se*, to govern the character of the Archetype of an Order. Only when their evidence is supported also by evidence under one of the four headings A-D above, have I deemed it permissible to use it in the construction of the Archetype. Thus, in forming the Archetype of the Order Lepidoptera, I have admitted only four branches to R_s , and have kept M_4 fused with Cu_{1a} right to their tips; since there is no evidence, apart from the atavistic specimens themselves, to show that these characters ever really belonged to the true Lepidoptera; whereas there is distinct evidence, in the form of the fossil record, to show that they did belong to Orders ancestral to the Lepidoptera.

Before entering upon the detailed researches that form the main portion of this paper, I desire to offer my very best thanks to all those kind friends who have made the work possible, by helping to supply the immense amount of material studied. Much of this material finds no mention in this paper, seeing that the limitations of space only permit of the use of the most telling arguments, which are reinforced, in the author's mind, by the results attained in many other directions, and with many other genera than those here mentioned. Thus I would ask those who supplied material, not to think that, because their particular specimens do not appear to fill any place in the argument, they were not of value. The number of dissections of pupæ in the Lepidoptera alone has approached two hundred, representing practically every family obtainable within a reasonable distance of Sydney, and not a few from distant localities. Let me, then, thank the following gentlemen for the supply of valuable material, mentioning here only the Orders involved; and let me make further special acknowledgments of those particular consignments, each in its proper place, which have proved of special value in this work:—Drs. T. A. Chapman, F.R.S., L. Perringuey and A. J. Turner (Lepidoptera), Messrs. Herbert Champion (Megaloptera), F. W. Carpenter (Planipennia, Trichoptera, and general help in the field), E. J. Dumigan (Lepidoptera), Luke Gallard (Planipennia, Lepidoptera, Diptera), G. H. Hardy (Diptera), G. Howes (Megaloptera, Trichoptera), G. Lyell (Lepidoptera, Mecoptera), E. Meyrick, F.R.S., (Lepidoptera), K. J. Morton (Trichoptera, Lepidoptera), A. Philpott (Lepidoptera), and the discoverers of the fine new types of three fossil Orders, Messrs. B. Dunstan and J. Mitchell.

Section i.—THE BASAL TRACHEATION OF THE PUPAL WING.

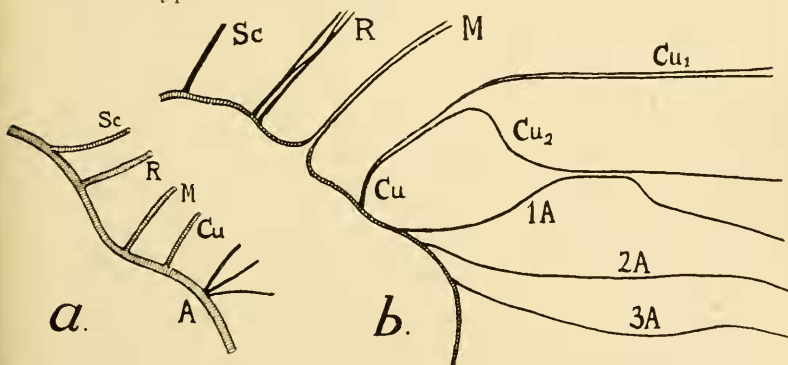
(Text-fig. 36.)

Comstock and Needham (14) have shown how, in the most primitive types of wings, the tracheal supply arises from two sources. An anterior trachea, called the *costo-radial trachea*, arises either from the dorsal trunk, or from the anterior branch of the Y-shaped leg-trachea, and enters the wing anteriorly. From this, the costal (if present), subcostal and radial tracheæ are derived, as well as, originally, the median trachea. A posterior trachea, called the *cubito-anal trachea*, arises either from further back along the dorsal trunk, or from the posterior branch

of the Y-shaped leg-trachea, and enters the wing posteriorly. From this, the cubital and anal tracheæ are derived. Originally there was no connection between the two groups of tracheæ; and this primitive condition is still preserved in the *Perlaria* and certain Cockroaches. But, in most other insects, the two groups are linked up by a short connecting-loop, so that a complete trachea, in the form of an arch, which I have called the *alar trunk* (18), lies at the base of the growing wing, and sends the main wing-tracheæ into it.

In the more archaic of those insects in which the alar trunk is complete, the median trachea may still belong to the costo-radial group. But, as specialisation proceeds, the base of the median trachea tends to move along the alar trunk posteriad, towards the cubito-anal group, and finally becomes incorporated in that group of tracheæ.

In the Panorpoïd Complex, we have, as already stated, three Orders only in which the wings are holotracheate, and three in which they are merotracheate. Let us examine the holotracheate types first.



Text-Fig. 36.

Basal Tracheation of the pupal wing in the Panorpoïd Complex. *a*, in Megaloptera and Planipennia; *b*, in a hindwing of *Charagia splendens* Scott, (Order Lepidoptera, fam. *Hepialidae*), to show the double origin of trachea M. Lettering on p. 535. (See also Plate xxxiii., fig. 20).

The condition to be found in both Megaloptera and Planipennia is that in which (Text-fig. 36, *a*) the alar trunk trachea is complete, and M stands about half-way between the costo-radial and cubito-anal groups of tracheæ.

The condition found in the higher Lepidoptera is well illustrated by Chapman, in Comstock's latest work (15, fig. 21). The genus figured is *Antheraea* (family *Saturniidae*), one of the most highly specialised of all Lepidoptera. In this type, as might have been expected, the alar trunk is complete, and the median trachea has migrated completely across to the cubito-anal group.

It seems obvious that the archetypic condition of the bases of the main tracheæ for the Lepidoptera ought not to be determined by the selection of such a highly specialised type as *Antheraea*. The *Hepialidae* and *Cossidae*, at any rate, might reasonably be expected to show a more primitive condition. Moreover, it is not yet really known by what means the connecting piece between the two main groups of tracheæ has been developed, nor by what exact method the media has migrated across it. I therefore paid careful attention to these points, when dissecting pupæ of the more archaic Lepidoptera.

In the *Cossidae*, I found, within the single genus *Xylentes*, much variation in the position of M. Sometimes it was close to the costo-radial group; sometimes close to the cubito-anal group; and less frequently it lay about half-way between them, much as in the *Planipennia*. In all cases, the alar trunk was complete.

In the *Hepialidae* (Text-fig. 36 *b*), I met with a very great surprise. In many pupal wings the alar trunk is not complete; but the two groups of tracheæ are brought together by the approximation of two large tracheæ, viz., the most posterior of the costo-radial group (this trachea should be M) and the most anterior of the cubito-anal group. These two tracheæ pass into the wing alongside one another, and together supply the branches of M.

Several pupæ of *Charagia* showed this condition, and I began to think that it might be the normal one for the family. However, further dissections showed that the condition was very variable. In some pupæ, the cubito-anal branch to M was very weakly formed, while the principal supply to M consisted of a huge trachea connected with the costo-radial group. This, I think, is probably the most archaic condition. The tendency towards the splitting-back of tracheæ towards their bases is very strong in all Lepidoptera. If then, we grant that the alar trunk was not completed in the ancestor of the Lepidoptera, it is easy to see how, when the tracheal connection from the cubito-anal

group grew out towards the base of the true median trachea (still united with the costo-radial group), it might have become connected, not with the single base of this trachea, but with the posterior half only, split back almost to its very base. This connection, once established, would give rise to the condition described above, in which M is supplied apparently by two strong tracheæ, one from each group.

Further dissections of pupæ of *Hepialidae* also revealed a number of instances in which the alar trunk was complete, although its middle portion is never strongly formed. In these cases, M was sometimes still closely connected with the costo-radial group, sometimes just as closely connected with the cubito-anal group.

The conclusion we must come to from this evidence is that, in the ancestor of the Lepidoptera, the alar trunk was not fully formed as a completed arch at the base of the wing. There was probably present a small tracheal outgrowth from the cubito-anal group, which, owing to the already strongly developed tendency of the main tracheæ to split back to their bases, did not always make the same connection with M; and so the various formations met with at the bases of Hepialid pupal wings must have been arrived at.

In so far as they have attained a moderate degree of specialisation, the alar trunk being complete, and the median trachea placed about half-way between the costo-radial and cubito-anal groups, both the Megaloptera and Planipennia must be considered as more specialised in this respect than the *Hepialidae*, and, therefore, than the archetype of the Lepidoptera. But the lines of evolution of these two Orders and of the Lepidoptera, for this character, are not the same. The tendency towards the splitting back of the trachea, which is in itself a specialisation in a different direction, is only developed to any great extent in the Lepidoptera; and, as we have seen, it was probably this line of specialisation that prevented the complete formation of the alar trunk in the earliest Lepidoptera. We might note, in this connection, that, in the *Jugo-frenata* (27), in which this splitting is not so strongly developed as in most Lepidoptera, the alar trunk is completed, though its middle portion is of small calibre.

Turning next to the Orders with merotracheate wings, we may take first of all the Diptera, in the older members of which

(Text-fig. 50) the reduction of the tracheation has only gone so far as to eliminate M and the anal tracheæ. In this Order, so far as known, the alar trunk is complete, but the middle portion of it is of very small calibre. The costo-radial group of tracheæ remains well developed except for the loss of M, and there is in most cases a definite *costal trachea* (C) present, running close up to the anterior border of the wing.

Much more specialised by the reduction of their pupal wing-tracheation, and, through this character, therefore, not ancestral to any other existing Order, are the Mecoptera and Trichoptera. In the former Order, the anal trunk is incomplete; the costo-radial group sends only one trachea into the wing, viz., R; and the cubito-anal group likewise only sends one, viz., M. If this latter trachea is the original M, then it would suggest that there must once have been a time when the alar trunk was complete, so that M might have migrated along it to the cubito-anal group, with which it is now connected. On the other hand, the basal portion of the cubital vein is much weakened in this Order; and it may be that the trachea grows out into the wing after the venational scheme is laid down. Hence, if the natural course along Cu is closed up, the trachea might be expected to penetrate the media instead. In whatever light we look at it, the condition of the pupal tracheation in this Order must be regarded as highly specialised.

The most specialised Order of all, as regards the condition of its pupal tracheation, is the Trichoptera. The alar trunk is incomplete, but, even in so old a group as the *Rhyacophilidae*, the costo-radial group sends only one trachea into the wing, usually along R, but sometimes apparently quite aimlessly, as if it were content to penetrate anywhere within the sheath; and the cubito-anal group is greatly reduced, sending only one weak trachea into the wing either along Cu or 1A, or aimlessly into the sheath, without any relationship to the venation.

Owing to the great reduction of the tracheation in these two last Orders, we cannot be sure that they may not have passed through a stage of development, in times past, in which the alar trunk was complete, though weakly formed. All we can assert with confidence is that their present condition is a very highly specialised one, and indicates a line of evolution, for this character, quite different from that of the three Orders with holotracheate wings.

We may sum up the above results as follows:—

(1) *Orders in which the pupal wings are holotracheate* :—

(A) Alar trunk not always quite complete; position of trachea M upon it variable; very strong tendency towards splitting back of all tracheæ.LEPIDOPTERA.

(B) Alar trunk complete; position of trachea M about midway along it between the costo-radial and cubito-anal groups; little or no tendency towards the splitting back of the tracheæ.....MEGALOPTERA and PLANIPENNIA.

(2) *Orders in which the pupal wings are merotracheate* :—

(C) Alar trunk complete; more than two tracheæ enter the wing; a true costal trachea frequently present.

.....DIPTERA.

(D) Alar trunk incomplete; only two tracheæ enter the wing, one from the costo-radial and one from the cubito-anal group; generally no costal trachea.*

(a) The anterior trachea is R, the posterior M.

.....MECOPTERA.

(b) The anterior trachea is R, the posterior Cu or 1A; or both may penetrate aimlessly into the wing-sheath.

.....TRICHOPTERA.

It will be clear, from the characters studied in this section alone, that the Trichoptera, as the most-highly specialised of all the Orders in the evolution of its pupal tracheation, cannot be regarded as ancestral to any other Order now existing. Nor can the Mecoptera possibly be ancestral to any Order except the Trichoptera; and this only by supposing that the Trichopterous condition could be naturally derived from the Mecopterous, as a further specialisation. As we shall see in the sequel, there is at least one venational character in which the Trichoptera are more archaic than the Mecoptera; and thus they cannot be derived from these latter.

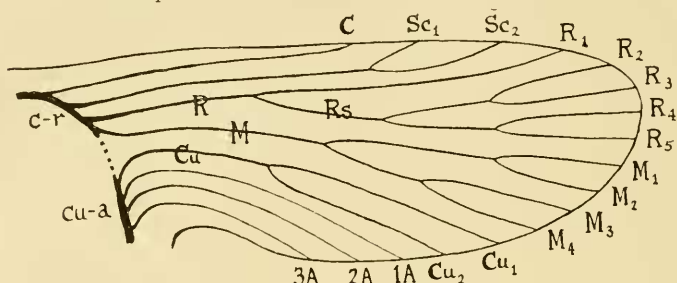
Section ii. THE MAIN VEINS AND THEIR BRANCHES.

(Text-figs. 37-40.)

In their hypothetical ancestral type of tracheation for the Insect Wing, and consequently also for the venation (which originally coincided with the tracheation in so far as the main veins were concerned), Comstock and Needham (14) indicated the following conditions for the tracheæ and veins:—

*I have seen a costal trachea in *imaginal wings* of some Trichoptera, but never in the pupal wings.

C (rarely present), simple; Sc, forked distally; R₁, simple; R_s, four-branched; M, four-branched; Cu, two-branched; 1A, 2A, 3A, all simple.



Text-Fig. 37.

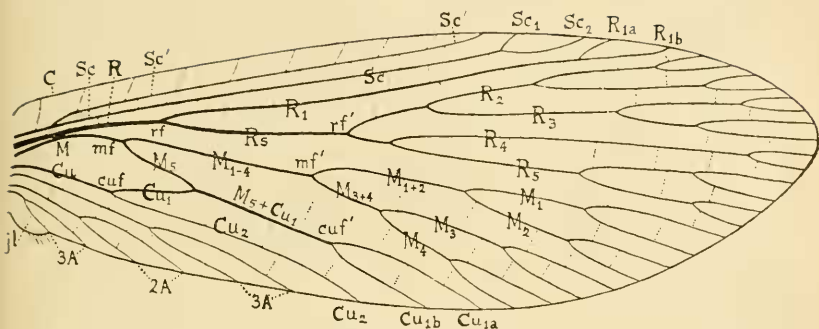
Hypothetical Type of Wing-venation, according to Comstock and Needham. (From Comstock). *c-r*, costo-radial basal trachea; *cu-a*, cubito-anal basal trachea. Other lettering as on p. 535.

This hypothetical type is shown in Text-fig. 37.

My attempt to apply this type of venation as archetypic for the Orders of the Panorpoïd Complex did not meet with success! and I was soon forced to conclude that this hypothetical type needs considerable alteration, before it can be accepted as typical for the original scheme of the wing-venation in these Orders. There is no doubt whatever about the correctness of the hypothetical arrangement of the tracheæ as having been originally in two groups entering the base of the wing separately, as will be seen from Section i. Nor can I find any flaw in Comstock's argument (15) as to the original *dichotomic* manner of arrangement of the branches of R and M. These points are accepted in this paper. But, with regard to the *number of branches of the main veins*, I am quite unable to accept Comstock's conclusions. In this Section, I propose to review briefly the evidence concerning the condition of branching of each main vein, in the Archetype of the Complex. Text-fig. 38 shows the venation of this Archetype, as worked out in full in this Part.

The Costa and the Subcosta.

A separate costal trachea is sometimes present in the pupal wing, as, for instance, in the Megaloptera (15, fig. 166) and in the Diptera (Text-fig. 50). In the fossil genus *Archipanorpa*,



Text-Fig. 38.

Venation of forewing of Archetype of the Panorpid Complex as worked out in this Part. (See also Text-fig. 111). Lettering as on p. 535. Note especially the fusion of M_5 with Cu_1 to form the cubito-medial Y-vein.

belonging to the Order Protomecoptera, I described a well-developed costal vein (5), and, in the fossil genus *Aristopsyche* of the Order Paratrachoptera (28), I also described a much-shortened costal vein near the base of the wing. Besides these, a strongly developed costal trachea may be found running along the anterior marginal vein in the imaginal wings of many Trichoptera and Diptera.

Further study of the fossils above mentioned has convinced me that the veins which I originally described as the costa are, in reality, only branches of Sc. In *Archipanorpa* (Text-fig. 64), the origin of this vein is missing. But it is *strongly concave*, like Sc below it; whereas a true costal vein should certainly be convex. In *Aristopsyche*, I have succeeded in tracing the supposed vein C back to a definite origin on Sc; so that this vein also must be considered as a shortened basal branch of the latter.

As it seems very likely that the marginal vein of Trichoptera and Diptera may be a secondary development, due to strengthening of the anterior border of the wing, I have decided to omit the question of the presence or absence of a true costal vein from the evidence used in constructing the Archetype. It seems, however, very unlikely that any true costal vein, distinct from the anterior border of the wing, was ever present in any Panorpid type, seeing that such a vein is absent from almost all known insect wings.

It follows, from the above, that the subcosta may be branched either basally or distally. The basal branching is complete in *Archipanorpa*, where Sc consists of two long concave veins, running side by side between R_1 and the anterior border of the wing. If this condition be altered, by reduction of the upper branch, we arrive at the stage shown in *Aristopsyche*, in which this branch is clearly becoming reduced to a mere veinlet. A comparison of Text-figs. 65, 85, will show clearly that the final fate of this branch is that it becomes the humeral veinlet (*hm*).

Besides this basal branch, Sc is frequently forked distally, as in Text-figs. 63, 76. This is certainly an archaic condition, and I have accepted it as such. As the usual notation for the distal forking is Sc_1 and Sc_2 , I have suggested the use of Sc' for the more anterior basal branch in *Archipanorpa* (Text-fig. 64) and in the Archetype of the Complex (Text-fig. 38). The archetypic condition, in which both Sc' and the distal forking are present together, has not been found so far in any single known type; but the condition in which the distal forking remains, while the basal branch is reduced to the humeral veinlet, is quite common.

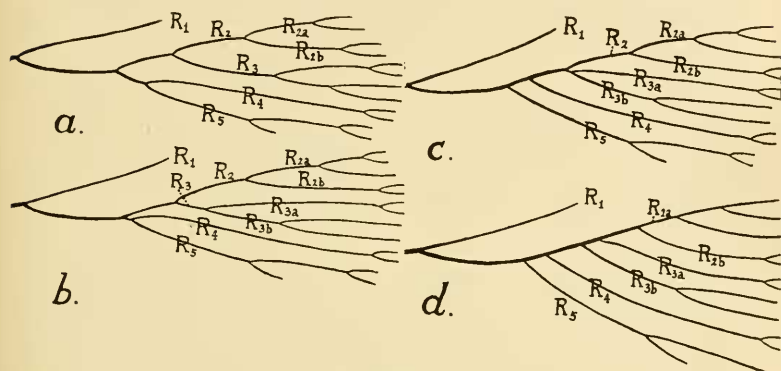
The Radius and Radial Sector.

The main stem of the radius (R) divides, in all archaic types, not far from the base of the wing, into a fairly simple upper branch (R_1) and a more complexly branched lower branch, called the *radial sector* (Rs). The point at which this division takes place is the *primary radial fork* (*rf*).

The most archaic condition of R_1 is clearly that in which it is a straight vein, with a definite distal forking into R_{1a} and R_{1b} , as seen in Text-figs. 63, 76. By loss of this terminal fork, it usually becomes a simple, straight vein.

Comstock has clearly shown (15) that the original condition of branching of Rs was dichotomic. His diagram showing how the pectinate type of branching of this vein can be derived from the older dichotomic type (15, fig. 138) unfortunately assumes that Rs was originally only four-branched. This is not borne out by the palaeontological evidence, at any rate as far as the Panorpoïd Complex is concerned. The number of branches of Rs in the more archaic representatives of each Order is fully worked out in those Sections devoted to the venations of the separate Orders (Sections viii.-xvi.) which should be referred to for details. It will suffice to state here that the evidence is overwhelmingly in favour of Rs having had more than four

branches originally in the Orders Mecoptera, Paramecoptera, Protomecoptera, Megaloptera and Planipennia; whereas, in the more specialised Orders Diptera, Trichoptera, and Lepidoptera, it is reduced to the four-branched condition. It will, of course, be perfectly obvious that the pectinate type of branching, which



Text-Fig. 39.

Stages in the evolution of the pectinate type of radial sector from original dichotomic type, shown in *a*. Lettering as on p. 535.

distinguishes Handlirsch's Sub-class Neuropteroidea from his Panorpoidea, is just as easily derived from a dichotomic condition with *more* than four branches, as it is from one with only four branches. Text-fig. 39 shows us how this could be brought about, starting with a dichotomic type in which the branches of Rs are arranged as in the Archetype of the Complex (Text-fig. 38). In this connection, I wish especially to draw attention to the position of the dichotomic forkings in the fossil genus *Belmontia* (Text-fig. 63), and to emphasise the obvious fact that a very little movement of the point of origin of R_4 , from its original position on R_{4+5} across to R_{2+3} would at once produce the pectinate type of branching.

The fossil *Belmontia* (Text-fig. 63) may not, however, be taken as the starting point of the Neuropteroid Orders, for two reasons. Firstly, *Belmontia* is clearly more specialised than the older Megaloptera in the reduction of the series of costal veinlets and the arrangement of its cross-veins, as well as, probably, in its simplified anal veins, and possibly also in the very complete formation of the cubito-median Y-vein (see Section iii.).

Secondly, a study of the Orders Megaloptera and Planipennia (Section xv., xvi.) shows us that the evolution of the pectinate type of branching of Rs was probably at first confined to R_{2+3} , the dichotomic condition of R_{4+5} remaining in these insects long after the rest of Rs had become pectinately branched.* Thus we are driven back to examine R_{2+3} only, and to try to discover what its original condition was, before it became pectinate.

A study of the wings of archaic Megaloptera and Planipennia must convince us that there were *more than two* original dichotomic branches of R_{2+3} concerned in the formation of the pectinate type. All the fossil Planipennia show a considerable number of pectinate branches in this region, and the same is true of most of the *Corydalidae*, all the *Ithonidae* and *Psychopsidae*, and most other archaic types. Even in the very reduced *Sisyridae* (Text-fig. 110), it must be clear that at least three branches of R_{2+3} took part in this formation. Probably the actual number of branches varied according to the size of the species affected. As an illustration of the manner in which pectination of Rs could be brought about, without loss of the original dichotomy of R_{4+5} , from a many-branched type, we have selected the actual type of branching found in *Archipanorpa* (Text-fig. 39), and have shown how, by very simple changes, the original dichotomies of R_{2+3} can be altered to the pectinate arrangement.

As the point at which Rs first forks is of great importance, we have called it the *secondary radial fork*, with the notation *rf'*.

The Media.

The original first dichotomy of this vein was clearly that into M_{1-4} and M_5 (Section iii.). This has hitherto been overlooked. The point at which this forking takes place is the true *primary median fork*, and should carry the notation *mf*. The point at which M_{1-4} divides into M_{1+2} and M_{3+4} , hitherto known as *mf*, must now be called the *secondary median fork*, and must take the notation *mf'*.

The evidence is clear that, in the three Orders Mecoptera,

*Note, however, that, if R_5 itself were originally branched, as in Text-fig. 38, R_4 might migrate across to R_{2+3} and still leave a branched vein in the original position of R_{4+5} . It is thus impossible to decide this point definitely.

Paramecoptera and Protomecoptera, M_{1-4} had more than four dichotomic branches originally. It is equally clear that, in the more specialised Orders Diptera, Trichoptera and Lepidoptera, this number was reduced to four. As regards the Megaloptera and Planipennia, the evidence is not conclusive one way or another. For, although the great majority of forms in these Orders have this vein reduced to four branches or less, yet the fossil *Kalligrammatidae* show it with from five to nine branches, while six branches can be counted in the hindwing of the recent *Megapsychops*. But these types are both of them Planipennian, and exceptionally abundantly veined. I have therefore assumed that the Orders Megaloptera and Planipennia had archetypically M_{1-4} with only four branches, though I think that more definite evidence on this point may be forthcoming later on from the fossil record.

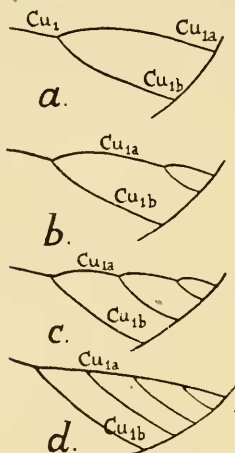
As regards the condition of M_5 , it is clear that the complete fusion of that vein with Cu_1 to form the cubito-median Y-vein, as in *Belmontia* (Text-fig. 63), is a very primitive condition. We are still in doubt, however, as to whether the state of this vein shown in certain primitive Megaloptera and Planipennia (Text-figs. 44, 45) is to be regarded as derivable from the condition seen in *Belmontia*, or whether it is a reduction from a more primitive formation, in which M_5 has not succeeded in becoming fused with Cu_1 . Until we have further evidence on that point, we cannot fix the geological age at which these Orders arose. This question is fully discussed in Section iii.

The Cubitus.

A special Section (Section iv.) has been devoted to this vein, as the condition of its branching is of the utmost importance in this research. The conclusions reached are that Cu was originally three-branched, Cu_1 having a distal forking into Cu_{1a} and Cu_{1b} , while Cu_2 was a weak concave vein. It is possible that the distal branching of Cu_1 may have been originally due to incomplete fusion of M_5 distally with that vein; but this point cannot be decided with certainty, in the absence of fossil evidence.

The *primary cubital fork* (*cuf*) is situated near the base of the wing, and is the point at which Cu divides into Cu_1 and Cu_2 . The *secondary cubital fork* (*cuf'*) is the point at which Cu_1 divides into Cu_{1a} and Cu_{1b} . This latter forking is present in all the Orders of the Complex, except only in the Mecoptera,

Paratrichoptera and Diptera, in which Cu_1 is a strong, straight vein, without any branches.



Text-Fig. 40.

Stages in the evolution of the pectinate type of first cubitus, from original dichotomic type shown in *a*.

In many Planipennia, and some Megaloptera, the original dichotomic forking of Cu_1 is replaced by a pectinate type of branching, due to additions from the tip inwards. The manner of evolution of this type is shown in Text-fig. 40.

The Anal Veins.

These also are dealt with in a special Section (Section v.). I have, however, omitted from that discussion any reference to the probable number of branches of these three veins. A study of the known venational types within the Complex fails to offer us any clear decision on the point, seeing that the branched condition of these veins seen in so many Megaloptera and Planipennia may be secondarily derived from the simple condition found in the Panorpoidea. I have, therefore, left this question in abeyance, though I have figured these veins in the Archetype of the Complex (Text-fig. 38) as branched, as I think that this is most likely to have been their primitive condition.

Section iii. THE ARCULUS AND CUBITO-MEDIAN Y-VEIN.

(Plate xxxi., figs. 15-16, and Text-figs. 41-45.)

The term *arculus* was originally applied, by writers on the Order Odonata, to the remarkable formation shown near the

base of the wings in that Order, R and M being fused basally, and then diverging further distad, so that M approaches Cu. The curve thus formed is completed by a strong cross-vein descending from M to Cu. The *arculus* consists of the curved portion of M, from the point at which it leaves R, to the top of this cross-vein, *plus* the cross-vein itself. The portion formed from M has been called the *anterior arculus*, that from the cross-vein the *posterior arculus* (Text-fig. 41a).

Comstock has extended the use of the term to other Orders also, in which somewhat similar formations are to be met with (15, p. 78). In the Trichoptera and Lepidoptera, in particular, he has applied the name *posterior arculus* to the supposed cross-vein that descends upon Cu_1 not far distad from the cubital fork.

The discovery of the fossil Order Paramecoptera (29) has shown us very clearly that this supposed cross-vein is not a cross-vein at all, but a true branch of M, whose existence might otherwise have passed unsuspected. As this discovery is of the utmost importance, for the right understanding of the Phylogeny of the Complex, it is necessary here to undertake a careful analysis of the region of the arculus, and to give the full proof of the true nature of this basal posterior branch of M, which has hitherto been regarded as a cross-vein.

In order to follow this argument clearly, it will be necessary to go back, first of all, to the Odonata, in which the arculus still exists in a more primitive condition than it does in any Order of the Panorpid Complex. In the Zygopterous Odonata, which preserve the most archaic condition of the venation as regards the media and its branches, there are actually *five* branches of M represented. But, owing to the fact that the venational scheme was worked out from the more specialised Anisoptera, in which Rs has crossed over M_1 and M_2 , and has captured the third branch (leaving its basal portion as the so-called *bridge-vein*), the notation originally applied to these five branches, beginning with the most anterior, was M_1 , M_2 , Rs, M_3 and M_4 respectively. When I pointed out that, in the Zygoptera, the supposed Rs was really a branch of M, I adopted the name Zygopterid Sector for it, with the notation Ms (19). Hence the notation for the five branches now stands at M_1 , M_2 , Ms, M_3 and M_4 respectively, the last three being actually the *third*, *fourth* and *fifth* of these branches, in order. The correct nota-

tion, of course, would be M_3 , M_4 and M_5 respectively for these three branches; and, as this is not an Odonatological research, I propose to use these terms in this paper.

A careful analysis of the Odonate areculus shows that it is really divisible into *three* parts, viz.:—

(i.) the uppermost part, from the point where M leaves R to the point where M_{1-4} diverges from M_5 .

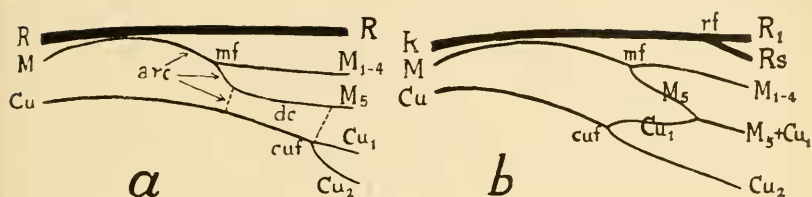
(ii.) the middle part, consisting of a short basal piece of M_5 from its divergence from M_{1-4} to the top of the cross-vein.

(iii.) the lowest part, formed from the cross-vein, called the *posterior areculus*.

The middle portion (ii.) is apt to be overlooked, since, in the majority of recent Odonata, M_{1-4} and M_5 come off together from the same point on the areculus; or, in other words, the cross-vein forming the lowest portion has moved up to the point of origin of M_5 , thus obliterating (ii.) altogether. But in some fossils this portion is the longest of the three, as, for instance, in *Aeschnidiopsis* (22). This middle part is of the greatest importance in the present discussion, and must not for one moment be lost sight of.

Lying distad from the posterior areculus, in the Zygoptera, is the discoidal cell, or quadrilateral, whose upper and lower sides are portions of M_5 and Cu respectively. The condition that this cell can be formed was laid down by me in a former work (21, p. 57), viz. that the bifurcation or forking of Cu must take place at some point distad from the level of the areculus. If the cubital fork were placed at some point closer to the base than the areculus is, no discoidal cell could be formed, and the evolution of the areculus would have to proceed along different lines.

Now, in all archaic types within the Panorpoïd Complex, the cubital fork lies very close to the base, and the areculus lies at a level somewhat distad from it. Hence it was not possible for a discoidal cell of the Odonate type to be formed, and the evolution of the areculus has proceeded upon different lines. Instead of remaining separated by a definite area, out of which in the Odonata, the discoidal cell and the area distad from it are formed, M_5 and Cu_1 have become more and more approximated, and very early became fused, for at least a considerable portion of their lengths, as we find them already in the Permian Paramecoptera. This condition is shown in Text-fig. 41, *b*. The



Text-Fig-41.

Diagrams to show the structure of the areculus and cubito-median Y-vein.

a, areculus in Odonata, with the discoidal cell or quadrilateral (*dc*) formed between two cross-veins; *b*, cubito-median Y-vein in the Panorpid Complex, formed by fusion of M_5 with Cu_1 . Lettering as on p.535.

resulting formation may be called the *cubito-median Y-vein*. Its relationship with the Odonate areculus will now be quite clear. Part (i.) of that areculus, defined above as the part of M from its divergence from R to the origin of M_5 , takes no part in it at all. Part (ii.) corresponds with the upper arm of the Y, in so far as it is the basal portion of M_5 ; it is not, however, terminated below by a cross-vein, but by the point of junction of Cu_1 with M_5 . Part (iii.), the cross-vein, is absent; if it were ever present, as is very probable, then it has been entirely eliminated by the fusion of M_5 with Cu_1 . The lower arm of the Y is the basal portion of Cu_1 , and corresponds with the same portion of the same vein in the Odonata, which, as we can see from Text-fig. 41*a*, lies distad from the discoidal cell.

The *cubito-median Y-vein*, then, in the Orders of the Panorpid Complex, is a specialisation akin to the areculus in the Odonata, and serving the same purpose of strengthening the venation at a point of stress near the base. It is, however, only partially homologous with it; and the condition necessary to its formation is the opposite of the condition for the formation of the Odonate quadrilateral, viz. that the cubital fork should lie at a level *nearer* to the base than does the distal part of the areculus itself.

The proof that the upper arm of the Y-vein in the Parameroptera is actually a main vein, i.e. M_5 , and not a cross-vein, may be given briefly as follows (see Plate xxxi., and Text-fig. 63):—

(*a*) As regards its *structure*, an examination of the fossil

shows that it is very strongly formed, and exactly resembles the other main veins near the base of the wing. All the true cross-veins are very weakly formed, and their impressions in the fossil are of quite a different type and intensity.

(b) As regards its *direction*, this is oblique, and concave to the base of the wing, i.e. exactly similar to that of the lower arm of the Y-vein, but on the other side of the axis of symmetry of the Y. We know for certain that the lower arm of the Y is Cu_1 , and not a cross-vein; there can, therefore, be no reason (outside of a bias present from a previous belief that the vein corresponding to the upper arm of the Y in other Orders is a cross-vein) why it could possibly be regarded as such in the Paramecoptera. In other words, if the wing of *Belmontia* had been an absolutely new type, with no close relatives amongst existing Orders, nobody would have suggested that the upper arm of the Y was a cross-vein.

(c) As regards its *connection* with the main stem of the Y-vein, this is even more direct and complete than is that of Cu_1 . This can be well seen from the photograph in Plate xxxi., fig. 15. Anybody who might be asked, with an unbiassed mind, to say which of the two arms of the Y-vein is most likely to be a cross-vein, assuming that one or the other of them must be such, would certainly indicate the lower arm, i.e. Cu_1 , from a study of its method of connection with the main stem.

(d) As regards the *presence or absence of macrotrichia*, this vein is most certainly part of a main vein. An examination of any one of the main veins in this fossil will show the sockets of macrotrichia clearly present, whereas no such structures can be seen upon any of the cross-veins. Several of these can be seen upon the lower arm of the Y, i.e. Cu_1 . Although the upper two-fifths of the upper arm of the Y is somewhat damaged, and not well preserved, yet two sockets can be clearly seen upon the lower three-fifths, thus proving that it carried macrotrichia, and must therefore have been a portion of a main vein. In Plate xxxi., fig. 16, the arrow points to one of the sockets on M_5 , while another on Cu_1 can be seen by following the stem of the arrow backwards.

(e) As regards the *alternate convexity and concavity* of the main veins, the fossil shows quite clearly that R and Cu are convex, M concave. Further distad, as in all Panorpooid wings in which the levels of these veins differ appreciably, M_{1+2}

remains concave, while M_{3+4} becomes slightly convex. Meanwhile, Cu_1 remains convex for its whole length, and thus we have two adjacent main veins, M_{3+4} and Cu_1 both of them convex. This points to the fact that a concave vein must have been suppressed between them. If the upper arm of the Y-vein be truly M_5 , then this interpretation fits in exactly with the present convexity and concavity of the veins; for M_5 is a concave vein, and must be the basal portion of the concave vein missing further distally between M_{3+4} and Cu_1 .

Thus we see that, on all five counts, the upper arm of the Y-vein is shown to be M_5 , and not a true cross-vein.

It is impossible to decide whether the distal forking of Cu_1 is due to incomplete fusion of this vein with M_5 or not. The latter being a concave vein, it may well be that it had already become too weak distally, before the basal fusion was accomplished, to be able to take any part in the more distal formation. An examination of the distal forking of Cu_1 shows that both branches are more or less convex; this evidence, then, so far as it goes, would indicate that both belonged originally to Cu_1 . I propose, therefore, to continue the notation Cu_{1a} and Cu_{1b} for these two branches, while leaving it quite open for anybody to consider the upper branch as the distal end of M_5 , not completely fused with Cu_1 , if he prefers that interpretation. That M_5 took some part in the formation of the main stem of the Y-vein there can be no doubt whatever, seeing how strongly formed this vein is at the fork of the Y. Consequently the correct notation for this vein is $M_5 + Cu_1$ in this fossil. If this be borne in mind, there does not seem to be any reason why the notation Cu_1 for the corresponding vein in recent Orders should not be maintained, seeing that the influence of M_5 in its formation has undoubtedly gradually decreased; until, at the present day, the only trachea supplying it in most pupal wings is that of Cu_1 itself.

We may now sum up the above evidence as follows:—

In the Permian fossil Order Paramecoptera, the cubito-median Y-vein is strongly formed, and consists of an upper arm, M_5 , a lower arm, Cu_1 , and a distal main stem $M_5 + Cu_1$, which does not extend to the wing-border, but forks again distally into Cu_{1a} and Cu_{1b} .

The further discussion of the evolution of the distal forking of Cu_1 will be found in Section iv., dealing with the eubitus.

Having now analysed the complete Y-vein formation in the Order Paramecoptera, let us trace its evolution through the other Orders of the Complex.

(1) *The Mecoptera.*

These may be taken first, as they are the only Order known to have existed alongside the Paramecoptera in Palæozoic times. Three stages in the evolution of the Y-vein are to be found within this Order:—

(a) In the pupal wing of *Chorista* (23), the Y-vein is complete, though the upper branch, M_5 , is shortened. It is very important to notice that, in spite of the fact that this Order has merotracheate wings, yet tracheæ R and M still exist, and from the latter trachea a small branch penetrates down the upper branch of the Y-vein. This seems to me to be very significant of the true nature of this vein. At the time that I described this pupal wing first (23), I had not studied the areculus-formation outside of the Odonata, and knew nothing of the Paramecoptera; hence I regarded this vein as a cross-vein, in spite of its trachea. The new evidence has compelled me to alter my opinion.

In the fossil genus *Stereochorista* (Upper Triassic, 28), the Y-vein may be seen completely formed.*

(b) In the forewing of the genus *Panorpa*, the upper branch of the Y becomes transverse, and takes on the appearance of a cross-vein. A similar condition is to be seen in the forewing of *Merope* (Text-fig. 62); but in this genus the lower branch of the Y is much shorter than the upper. It is a pity that the pupal wing of *Panorpa* has so far not been examined as to the condition of M_5 , especially during the first day or two of pupal life.

(c) In the hindwings of the *Meropidae* and *Panorpidæ*, and in both fore and hindwings of the *Choristidae*, *Nannochoristidae* and *Bittacidae*, the upper branch of the Y becomes eliminated, and there is a greater or less degree of fusion between M_{1-4} and Cu_1 . It will be seen that this high degree of specialisation is not confined to the Mecoptera, but also characterises the majority of forms in the Trichoptera and Diptera, as well as certain groups in the Megaloptera.

*Since this was written, Mr. J. Mitchell has forwarded to me from the Upper Permian Beds of Belmont, a new type of Mecopterous wing with the Y-vein present.

[The region of the cubito-median Y-vein not having been preserved in the Triassic Protomecoptera, this Order has to be omitted from the discussion.]

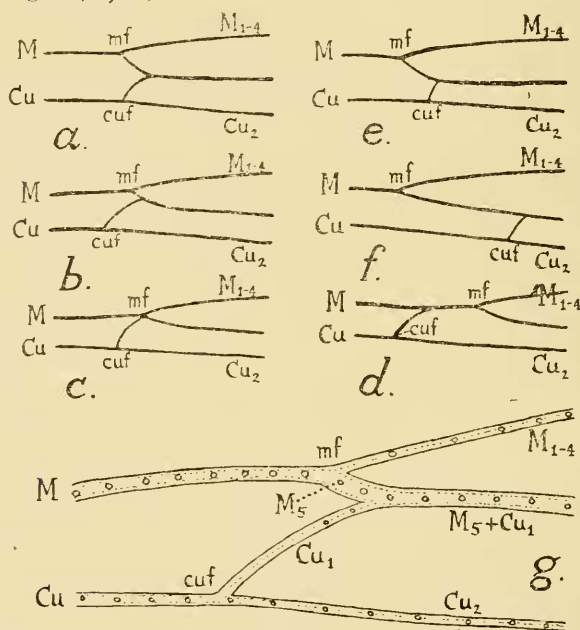
(2) *The Trichoptera.*

In this Order, the three stages indicated above for the evolution of the Y-vein in the Mecoptera are also to be found. The first, or most archaic, stage, is to be seen in a number of genera within the family *Rhyacophilidae*, as, for instance, in *Glossosoma*, *Mystrophora*, *Agapetus* and *Catagapetus*, as well as in certain species of *Rhyacophila* itself (Text-fig. 42, *a*). In some species there is actually a tendency for the lower arm of the Y-vein, Cu_1 , to assume the appearance and direction of a cross-vein, while the upper arm, M_5 , remains primitively oblique in position, and is longer than the lower arm. * This tendency leads to a new line of specialisation, not represented within the Mecoptera, in which the upper arm of the Y becomes further lengthened, as in the forewing of the undescribed species shown in Text-fig. 42, *f*. The most exaggerated condition of this line of evolution is to be found in certain *Hydropsychidae*, as, for instance, in *Hydromanicus* (15, fig. 322). It is due to a migration of the cubital fork distad, so that the main stem of the Y becomes much shortened, while its upper arm lengthens out.

Further proof that the upper arm of the Y-vein is a true main vein, and not a cross-vein, is to be obtained by a study of the trichiation in the genus *Rhyacophila*. Text-fig. 42, *g*, shows the trichiation of the Y-vein in *Rhyacophila dorsalis* Curtis. The lower arm, Cu_1 is weakened, and has lost all its macrotrichia, except one near the fork. The upper arm, M_5 , however, shortened though it be in this species, still carries macrotrichia, and has all the appearance of a part of a true main vein.

The figure of *Rhyacophila dorsalis* (Text-fig. 42, *b*) will serve to illustrate the second stage of evolution of the Y-vein in this Order, in which M_5 becomes definitely shortened. *Rh. fuscula* (Comstock, 15, fig. 320) shows a condition intermediate between the archaic, complete Y-vein, with the two arms approximately equal and symmetrical, and the stage shown in *Rh. dorsalis*. The third stage in the evolution of the Y-vein may also be seen in certain species of *Rhyacophila* (see Comstock, 15, fig. 321), the upper arm of the Y becoming obliterated, and M_{1-4} being fused with Cu_1 , either at a point, or for a short distance.

As in the Mecoptera, this last stage has become, for recent Trichoptera, the dominant condition throughout the Order. (Text-fig. 42, *c*, *d*.)



Text-Fig. 42.

Evolution of the cubito-median Y-vein in Trichoptera. *a*, *b*, *c*, *d*, successive stages in its reduction, leading to strong fusion of Cu_1 with M_{1-4} , as in *d*; *e*, *f*, stages in its lengthening; *g*, the same stage as in *b*, from *Rhyacophila dorsalis* Curtis, enlarged to show the distribution of the macrotrichial sockets. Lettering as on p. 535.

[Not enough is known of the condition of the Y-vein in the Triassic Paratrachoptera to furnish evidence of appreciable value in this discussion. The only genus in which it is partially preserved is *Aristopsyche* (28), in which it would appear that M_{1-4} was already partially fused with Cu_1 .]

(3) The Lepidoptera.

In this Order, the original condition of the Y-vein may be seen complete in many of the *Micropterygidae*, as already de-

scribed and figured (26). There is, however, no precedent trachea in M_5 in the pupal wing, and the main stem of the Y is supplied only by the trachea Cu_1 .

The same condition is to be found in the pupal wings of *Hepialidae*, of which I have dissected out a large number for the purposes of this paper. Pupæ of the following genera have been dissected: *Leto*, *Charagia*, *Porina* and *Oncopera*, the two latter being supplied by Mr. G. Lyell of Gisborne, Vic. In all of these the condition of the Y-vein is the same, viz. M_5 is represented by a pale band without any underlying trachea, while the trachea supplying the main stem of the Y is derived from Cu_1 . (Text-figs. 77, 79.)

The only pupal wings in which any sign of trachea M_5 can be detected are those of *Xyleutes* (fam. *Cossidae*). In two of the five pupæ which I dissected, a short but stout branch of M was to be seen arising near the base, and proceeding distad, below the main stem of M, towards the pale band which represents the upper arm of the Y, and which, in this genus, is transversely placed, resembling a cross-vein. It is possible that this trachea may be the lost trachea belonging to M_5 .

In advanced pupæ, I have sometimes found a fairly large trachea in M_5 ; but this is exceptional, as far as my experience goes. In no case have I seen this trachea penetrate far along the main stem of the Y-vein.

The conditions in the freshly emerged imago, of which I have examined a very large number, are very different from those of the pupa. A very strong trachea arises from M, and, passing down M_5 , supplies the main stem of the Y-vein right to its distal ends. The original cubital trachea which is found in this vein in the pupa, is often completely ousted, and its truncated remains may frequently be seen near the base of the wing, as in the case of *Wingia* (fam. *Oecophoridae*, Text-figs. 91, 92). It is, therefore, necessary to conclude that the main change takes place at, or very near, metamorphosis, at the same time that M_5 becomes a strongly chitinated vein, and the base of Cu becomes almost completely aborted.

It should also be noted that, in the *Hepialidae*, the condition of the tracheation in the freshly formed imaginal wing is very variable. Comstock (15, p. 328) states that, in all the wings of this family examined by him, M_5 (which he calls the *posterior arculus*) "is traversed by a branch of the median trachea,

which extends towards the margin of the wing in the longitudinal part of the cubitus, and parallel with the cubital trachea." In other words, both trachea M_5 and trachea Cu_1 are present in this family,—a condition which may be taken as more primitive than that mentioned above for *Wingia*, and found also in many other Lepidoptera. But an examination which I made of the freshly formed imaginal wings of seven Australian genera of *Hepialidae* (*Leto*, *Charagia*, *Pielus*, *Pörina*, *Perissectis*, *Oncopera* and *Fraus*), shows that this condition, though frequently present, is not by any means a constant. Trachea M_5 was found to be frequently of weaker calibre than trachea Cu_1 ; and there were a few extreme cases in which it had failed to develop much beyond the confines of the upper arm of the Y. In one extreme case (in a specimen of *Charagia splendens* Scott) it was altogether absent, so that the tracheation of this region of the imaginal wing was the same as that of the pupa.

Comstock (15, p. 328) suggests that the trachea which develops along Cu_1 in the imaginal wing, via M_5 (his "posterior areculus"), may be the missing trachea M_4 , split back in the same manner that the other tracheæ frequently are in the Lepidoptera. This suggestion cannot be entertained for one moment, for the simple reason that, in many imaginal wings which I have examined, trachea M_4 is present in its natural position, leaving M_{3+4} much further distad along the wing, and descending the upper branch of the distal Y-vein, formed by fusion of M_4 with Cu_{1a} , which is characteristic of the Order Lepidoptera. This formation is fully dealt with in Section vi.

In the great majority of the Lepidoptera, the evolution of the cubito-median Y-vein follows a single definite line, viz. the tendency to strengthen the upper arm, M_5 , at the expense of the lower, Cu_1 . The result of this is that, in all the higher families, the connection of the main part of vein Cu_1 with the true cubital fork is quite lost, and this vein is continued back more or less directly, via M_5 , to the main stem of M. A reference to Text-fig. 91 shows that, in such forms as *Wingia*, M_5 and Cu_1 are not yet completely aligned. In the highest types, the venation at the base of the wing becomes greatly thickened, and the serial vein formed from M_5 and Cu_1 becomes of great strength, and runs perfectly straight from its base to its secondary or distal forking, as in *Euschemon* (Text-fig. 100).

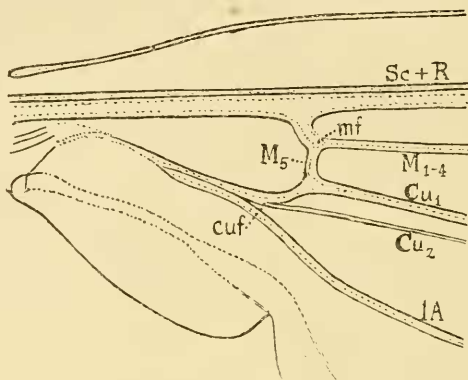
Reviewing the above evidence, we are bound to assume that, at the very beginning of the evolution of the Order Lepidoptera, M_5 had already begun to undergo some amount of degradation from its original condition of a normal main vein preceded by a trachea. That this degradation had not, perhaps, proceeded very far, is indicated by the frequent redevelopment of the trachea M_5 at metamorphosis. The condition seen in many imagines of the *Hepialidae*, in which *two* tracheæ traverse the vein Cu_1 , must be held to be more archaic than the commoner condition, in which only a single trachea, viz. that arising from M via M_5 , is to be found in this vein. The whole line of evolution seems to me to be exactly paralleled by the similar development in the evolution of the distal Y-vein, which is dealt with in Section vi. In fact, the normal method of reduction of the number of main veins by fusion, in the Panorpid Complex, is that of the *formation of Y-veins* of the type discussed in this section. Other examples of such formations are, of course, the fusion of M_{3+4} with Cu_1 in forewings of the Myrmeleontoid groups of the Order Planipennia (in which case the upper arm of the Y becomes the *oblique vein*), and the fusion of $1A$ with Cu_2 in the hindwings of Mecoptera, Trichoptera, Lepidoptera, and some Megaloptera. This latter fusion is dealt with under Section v.

(4) *The Diptera.*

In this Order, as in the Mecoptera and Trichoptera, our study is handicapped by the incompleteness of the pupal tracheation. It is not at all easy to obtain pupæ of archaic Diptera in the right condition for studying the tracheation of the wings. In the few which I have so far examined, there is no sign whatever of the median trachea; though I have found no less than *four* distinct trachea (C , Sc , R and Cu) all well developed in the wing of the Bombyliid *Comptosia* (Text-fig. 50).

In most Diptera, it would appear clear enough that the stage of fusion between M_{1-4} and Cu_1 , already described as the third stage in the evolution of the Y-vein in the *Rhyacophilidae*, had already been reached. But some of the more archaic families show definite evidence of an earlier stage of evolution, the upper arm of the Y (M_5) being present in the form of a shortened transverse vein, corresponding fairly closely with

the second stage of evolution in *Rhyacophila*, but more transversely placed. This condition is illustrated very well in the Stratiomyiid genus *Sargus* (Text-fig. 43) and others of the same family. I do not know of any Dipteron in which the



Text-Fig. 43.

Base of wing of *Sargus* sp. (Order Diptera, fam. *Stratiomyiidae*), to show presence of reduced cubito-median Y-vein. Lettering as on p. 535.

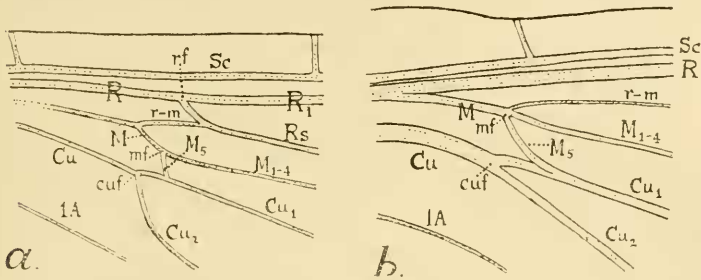
complete archaic form of the Y-vein can be made out; though I think that it may well be visible in the pupæ of some of the older types, which have not yet been obtained. Thus the evidence in this Order, though containing nothing *against* the supposition that the evolution of the Y-vein has been along the same lines as in the Trichoptera, is still not by any means as complete as we could wish.

(5) *The Megaloptera.*

In this order we meet with a peculiar position. In the more advanced groups, viz. the Raphidioidea and the family *Sialidae* of the Suborder Sialoidea, the forewing shows always a more or less complete fusion of M_{1-4} with Cu_1 basally, as in the third stage of evolution of the areculus in the *Rhyacophilidae* (Text-fig. 42, *d*). In the hindwing, the Y-vein is still evident, though its branches are generally much shortened, and M_5 appears as a very short vein. This condition is shown in Text-fig. 44, *a*, drawn from the archaic Sialid genus *Stenosialis*.

Turning to the family *Corydalidae*, which is generally admitted to be the most archaic family in the Order, and from

which, therefore, we might expect some light on the problem, we are surprised to find that there does not appear to be any basal connection at all between M and Cu in the forewing,



Text-Fig. 44.

Cubito-median Y-vein in hindwings of Megaloptera. *a*, from *Stenosialis* sp. (fam. *Sialidae*); *b*, from *Archichauliodes guttiferus* (Walk.), (fam. *Corydalidae*). Lettering as on p. 535.

except by means of an apparent cross-vein situated usually just *before* the cubital fork, and therefore not in the position in which one would expect to find M_5 , even if it were reduced to a cross-vein in form. In the hindwing, on the other hand, the Y-vein, though small, is quite completely formed in *Archichauliodes* (Text-fig. 44, *b*); and this condition is exactly that from which the somewhat more advanced stage already figured in *Stenosialis* can easily be derived.

We have to ask ourselves, then, whether the stage found in the forewing of the *Corydalidae* is due to the shifting basad of vein M_5 , after reduction to a transverse vein, or whether, perhaps, M_5 never existed as a main vein in the forewings of this Order. or whether there may be some further explanation of the case. Remembering how closely allied the Megaloptera are to the Planipennia, we may well turn to these latter for enlightenment, before we make a final judgment.

(6) *The Planipennia.*

Nearly all of these show no sign of M_5 , either in the fore- or in the hindwing. It would be easy to conclude that M_5 had never existed in this Order. However, in the course of my study of a fine Triassic Prohemerobiid (28), I came across what appeared to be a distinct vein in the position of M_5 . As this fossil, *Archepsychops*, is clearly allied to the recent

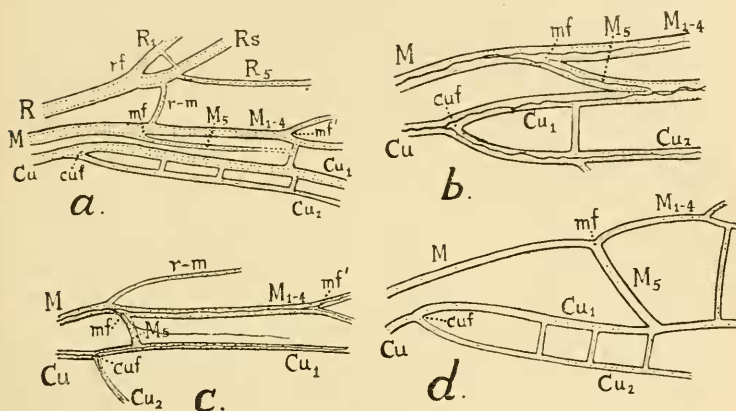
Psychopsidae, I turned to that family for further evidence. The result was the discovery, both in *Megapsychops illidgei* and in *Psychopsis elegans*, of the vein M_5 in its original position, but not strongly connected with Cu_1 . This condition is shown in Text-fig. 45a. The cubito-median Y-vein is not fully formed, in so far as M_5 weakens distally as it approaches Cu_1 . M_5 is also more parallel to Cr_1 than in the normal formation, and is sometimes connected with it by one or more cross-veins.

It is not possible to decide definitely whether the condition found in the Planipennia is a reduction from a more archaic stage than that seen in *Belmontia* (Text-fig. 41b), or whether it is due to the effect of a large addition of branches of Rs crowding the older veins together, so that M_5 and Cu_1 , though originally forming a Y-vein, have become pressed together in the manner now shown. The evidence from the hindwings would incline us towards the latter supposition, but the point is by no means certain. As the Megaloptera and Planipennia are more archaic than *Belmontia* in certain other venational characters, such as the complete system of costal veinlets, it may well be that the condition of M_5 in the forewing is really due to debasement of this vein from an older stage in which it ran freely between M_{1-4} and Cu_1 , without having attained any definite fusion with the latter vein such as we find in *Belmontia*.

An examination of the hindwings of various archaic types in the Order Planipennia shows that M_5 is generally present, and easily recognised owing to its oblique position, and the very evident forking of M which gives rise to it. Thus, we may take as an example *Osmylus* (family *Osmylidae*), in the hindwing of which (Text-fig. 45, d) the median fork is particularly well developed, with M_5 as a very strong oblique vein descending on to Cu_1 . In the *Psychopsidae*, the trachea supplying M_5 persists in the imago, and passes some distance along Cu_1 , thus offering an interesting parallel to the case of the Lepidoptera already discussed. In the American genus *Polystoechotes* (family *Polystoechotidae*) the trachea traverses the base of M_5 only, then leaves it, and runs freely in the membrane between M and Cu for a considerable distance (Text-fig. 45, c). This is an interesting survival, in view of the condition found in the forewing of *Psychopsidae*, dealt with above.

In the Planipennia in general, the chitinisation of the base

of M is very weak; and this vein is represented at its base, in many forms, by little more than its trachea. In others it is more strongly chitinated; but in no case does the typical main-



Text-Fig. 45.

Cubito-median Y-vein in the Order Planipennia. *a*, from forewing of *Megapsychops illidgei* Frogg. (fam. *Psychopsidae*); *b*, from hindwing of same; *c*, from hindwing of *Polystoechotes punctatus* Say, (fam. *Polystoechotidae*); *d*, from *Osmylus chrysops* (Linn.). (fam. *Osmylidae*). Lettering as on p. 535.

vein armature of macrotrichia begin on M until well past the position of M_5 . Thus we cannot, unfortunately, apply the test of the presence or absence of macrotrichia to M_5 in this Order.

The conclusion we are bound to come to is that, in the Planipennia and Megaloptera, M_5 was originally present. The specialisations it has undergone, especially in the forewing, are due to the development of the many-branched Rs in these Orders causing a correlated narrowing of the area supplied by M. The general result has been that M has become squeezed into a narrow space between the two strong convex veins R and Cu, and M_5 has therefore tended to become reduced, and finally obliterated in the forewing, though remaining more normal in the hind.

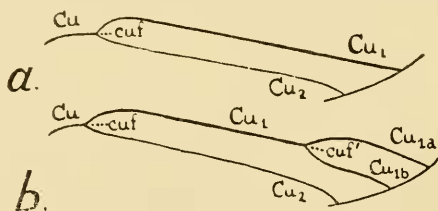
Section iv. THE STRUCTURE OF THE CUBITUS.

(Plate xxxii., fig. 17, Plate xxxiii., figs. 19-20, Plate xxxiv., figs. 21-22, Plate xxxv., fig. 23, and Text-figs. 46-50).

Before we can arrive at a correct conclusion with respect to the archetypic venation of any of the Panorpooid Orders, it is very necessary that we should study the cubital vein with special care, seeing that, on this point more than anywhere else, errors have been allowed to creep in, in the work of the Comstock-Needham school.

Comstock has assumed (15) for the Lepidoptera and Trichoptera, that the cubitus is two-branched, thus making this vein conform, in these two Orders, with his theoretical type. The fact that three branches can be clearly seen in the tracheation of the pupal wing, in all archaic Lepidoptera, is then explained by saying that the first anal trachea has migrated over to the cubitus, and fused with it entirely for its basal portion. The same explanation is given for an exactly similar occurrence in the Homoptera. But it does not seem to have occurred to the author of this extraordinary statement, that a careful comparative study of the veins in question, with the same veins in other Orders closely allied to them, might have offered a much more simple and obvious explanation, viz. that the cubitus is really three-branched, and the first analis remains in its usual position. Yet such is, as a matter of fact, the case, and the proof thereof is a very simple one.

Text-fig. 46*a* shows the form of Cu in the Orders Mecoptera, Paratrachoptera and Diptera. The cubital fork lies close to the



Text-Fig. 46.

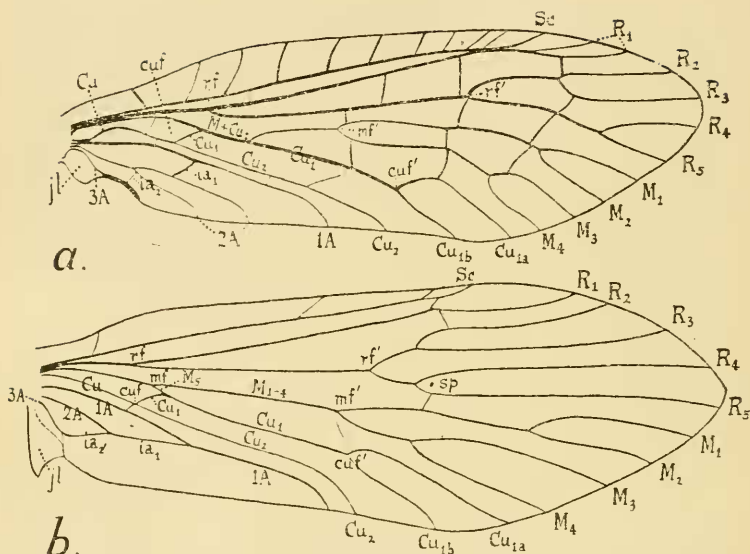
Structure of the cubitus in the Panorpooid Complex. *a*, the two-branched type found in Mecoptera, Paratrachoptera and Diptera; *b*, the original three-branched type found in the other Orders of the Complex. Lettering as on p. 535.

base of the wing; and the two branches, Cu_1 and Cu_2 , extend nearly parallel to one another, without any further branching. The anterior branch is, as always within the Complex, a strong, convex vein, easily picked out as of almost equal calibre with R, and much more strongly built than any other main vein. The posterior branch, Cu_2 , on the other hand, is a very weak, concave vein; in the more specialised types, it tends to sink completely into the anal furrow, and may cease to become chitinated, either altogether or in part, as in many Lepidoptera.

It is necessary to note here that Comstock admits this interpretation of the limits of Cu for the Mecoptera. There is, of course, no doubt about the matter at all in that Order.

Text-fig. 46b shows the form of Cu in the Orders Paramecoptera, Protomecoptera, Megaloptera, Trichoptera and Lepidoptera. One of these Orders, viz. the Megaloptera, has holotracheate wings; and hence we are able to examine the structure of the cubital trachea in the pupa. This corresponds exactly with the imaginal venation. Comstock himself figures the tracheation of the pupal wing of *Chauliodes* (15, fig. 170) with the three branches, labelling them Cu_1 , Cu_{1a} and Cu_2 . But, owing to the fact that he treats the Megaloptera as a portion of the Order Neuroptera, the other part being the Planipennia, he fails to give due prominence to this Order, and has missed the valuable evidence contained in its special type of wing-venation. The form of Cu in the Permian Paramecoptera agrees exactly with that of the Megaloptera, and so does that found in the Triassic Protomecoptera, as far as it is preserved. Thus there can be no doubt as to the antiquity of the extra branch of Cu_1 , which dates back to Permian times. As we have already seen in Section iii., the forking of Cu_1 may have been originally due to incomplete fusion of M_5 with Cu_1 distally. But, whether that be so or not, the fact remains that the *true primary cubital fork (cuf)* is not this fork at all, but the point at which Cu originally forked, i.e. much nearer to the base of the wing. All this is admitted by Comstock, as shown by his notation of the wings of Megaloptera (15, figs. 163-169).

Let us now turn to the case of the Trichoptera and Lepidoptera. Text-fig. 47 shows the complete venations of the forewings of the Megalopteron *Austrosialis* and the Trichopteron *Rhyacophila*. The former wing is holotracheate, the latter merotracheate; hence we cannot compare their tracheations.



Text-Fig. 47.

Comparison of the venation of a Megalopteron (*Austrosialis ignicollis* Till., fig. a) with a Trichopteron (*Rhyacophila dorsalis* Curtis, fig. b), forewings only, to show the similar structure of the cubitus. Note the strong fusion of M_{1-4} with Cu_1 in *Austrosialis*, and the double fusion of the anal veins in *Rhyacophila*. Lettering as on p. 535.

But, knowing the truth as regards *Austrosialis*, we can compare its imaginal venation with that of *Rhyacophila*. We then find that the two venational types agree in practically every detail of the courses and branchings of their main veins, and only differ in the number and arrangement of their cross-veins and veinlets, and in the fact that the Trichopteron shows a high specialisation of the anal area, (viz. the looping-up of the three anal veins), which is absent in the Megalopteron. The correspondence between the venations of the hindwings of the two types is even closer, but need not be figured here. There can, I think, be no doubt whatever that the cubitus in the Trichoptera is three-branched, as in the Megaloptera.

If, finally, we turn to the Lepidoptera, we find that the cubitus in this Order is of the same type as that seen in the

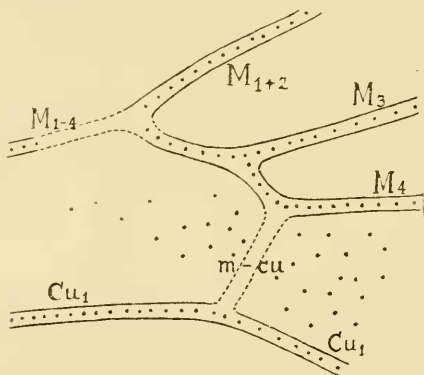
Trichoptera and Megaloptera. Examining the preceding pupal tracheation, we find that this also agrees exactly with the Megalopteran scheme. Where all the evidence from fossils, tracheation and venation alike, agrees exactly, where is the need to invent an explanation such as that given by Comstock, the only merit of which, as far as I can see, is *apparently*, but not actually, to bring the venation into line with Comstock's hypothetical type. For it should be noted that, in making the cubitus two-branched, to conform with this type, Comstock transfers the primary cubital fork to the position of the secondary fork, far distad along the cubital vein; yet he makes no effort to explain how it comes about that such a high specialisation should have taken place, within the limits of a considerable number of Orders.

Further proof of the correctness of the above evidence may be obtained outside the limits of the Panorpid Complex, by examination of the nymphal wings in the Hemimetabolous Orders Psocoptera and Homoptera, in which the cubitus has been interpreted as being two-branched by Comstock. I have examined the last three consecutive instars in *Psocus*, and the last two in a *Cicada*; and in all these instars the supposed 1A is truly a branch of Cu. If it were really 1A, we can scarcely suppose that so early a stage as the antepenultimate nymphal instar, in an ancient Order like the Psocoptera, would show the specialised fusing already complete. If it did, then our faith in the value of the Comstock-Needham System must be completely shattered, seeing that there would be no telling whether, for instance, Rs might not be really part of M, or M two separate veins fused together. It would only be necessary to explain that a fusion had taken place anywhere, and the venational scheme could be altered *ad infinitum*!

The evidence, then, seems to admit of no doubt whatever. Within the Panorpid Complex, the cubitus is three-branched in the Orders Paramecoptera, Protomecoptera, Megaloptera, Trichoptera and Lepidoptera; while in the Mecoptera, Paratrichoptera and Diptera it is only two-branched. In all the above Orders, the true primary cubital fork is the more basal forking of that vein. The extra fork, when present, belongs to Cu₁, and may or may not have been caused by incomplete distal fusion between M₅ and Cu₁ when the Y-vein of the areculus was

formed. In any case, the two-branched condition must be the more specialised. For, if M_5 had any part in the formation, then the complete fusion, which brought about the two-branched condition, is more specialised than the partial fusion, which left the three-branched condition. But, if M_5 did not extend so far distally, and if the whole formation belongs to Cu, then the natural explanation would be that the Mecoptera, Paratrichoptera and Diptera had lost the fork, which all the other Orders have retained.

Finally, it is necessary to add a word or two about the limits of Cu in the Diptera. Text-fig. 48 shows the cubitus and por-

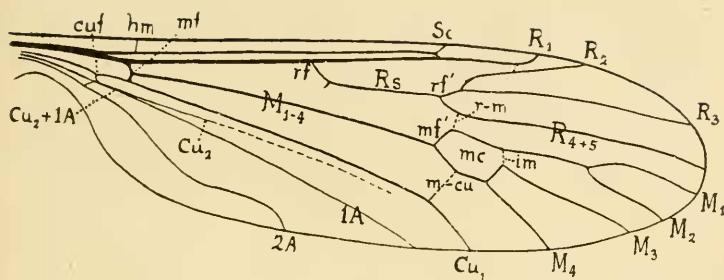


Text-Fig. 48.

Structure of the media and cubitus in the forewing of a Dipteran, *Rhyphus brevis* Walk. (fam. *Rhyphidae*). The true medio-cubital cross-vein, *m-cu*, carries no macrotrichia. Lettering as on p. 535. (x 87.)

tion of the media in the archaic *Rhyphus*, with the trichiation *in situ*. It will be seen that the vein named by Comstock Cu_1 (15, fig. 357) is really M_4 , the basal portion connecting it with Cu proper being a true cross-vein, without any macrotrichia, while the short piece connecting it with M, which Comstock names the cross-vein *m-cu*, carries strong macrotrichia, and is therefore the true basal portion of the main vein, M_4 .

Further evidence on the same lines may be obtained by a study of certain archaic Tipulid genera, such as the Australian *Gynoplistia*, in which the original position of the branches of

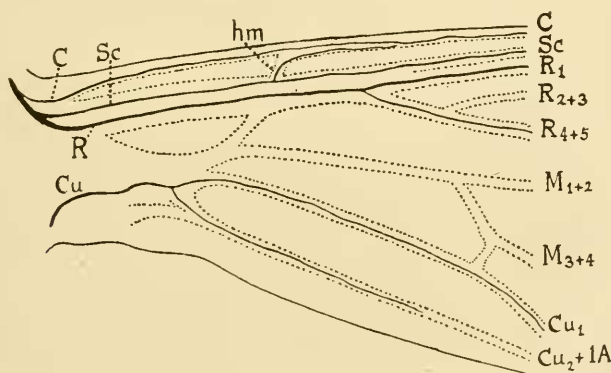


Text-Fig. 49.

Gynoplistia bella (Walk.) (Order Diptera, fam. *Tipulidae*) forewing showing the structure of the media and cubitus. Lettering as on p. 535.

M are retained. Text-fig. 49 shows very clearly that the interpretation of the veins given above for *Rhyphus* is correct, not only because Cu_1 is clearly simple in this ancient type, but also because M^4 comes off directly from the median cell (*mc*).

In the introductory part of this paper, we remarked that the tracheation of the pupal wing sometimes offered valuable evidence, even in the case of a merotracheate type. Text-fig.



Text-Fig. 50.

Base of pupal wing of *Comptosia* sp. (Order Diptera, fam. *Bombyliidae*) dissected out from sheath, just before metamorphosis, to show the merotracheate condition, and the complete cubital trachea. (x 36). Lettering as on p. 535.

50 shows the base of the pupal wing in a species of the Bombyliid genus *Comptosia*. Only the median and anal tracheæ are missing. The cubital trachea is complete, and shows the cubital fork situated at the extreme base of the wing, with Cu_2 apparently fused with 1A almost for its entire length. Thus not only is the above interpretation of the limits of Cu_1 correct, but we see also that the vein called 2A by Comstock (15, fig. 368) is in reality Cu_2+1A in this genus.

Section v. THE ANAL VEINS.

(Plate xxxiii., figs. 19-20, Plate xxxiv., fig. 22, and Text-figs. 51-54.)

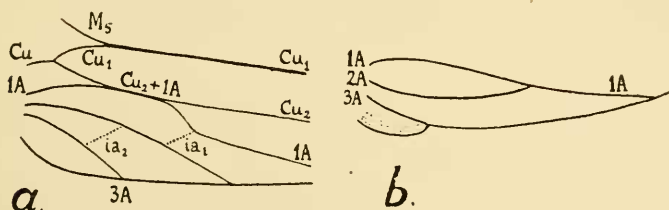
Throughout the Panorpoïd Complex, the anal veins are normally three in number, viz. 1A, 2A and 3A. These three veins are all normally convex, the membrane between them being usually more or less concave, and sometimes carrying definite grooves or furrows, which do not, however, carry true veins in them.

The anal tracheæ in the freshly-turned pupa stand in a group by themselves, and are easily recognised by their comparatively small calibre, and by the fact that they usually lie well apart from the cubitus. Corresponding with the sizes of the areas which they serve, the first analis is normally the largest of the three, the second of intermediate size, and the third the smallest. Exceptions to this rule occur when the first or second analis becomes shortened in the formation of a basal Y-vein; or when, owing to expansion of the anal area of the hindwing, both 2A and 3A may become very much lengthened, so as to be of approximately the same length as 1A.

Reductions in the number of anal veins from the normal three are only found in specialised types within the various Orders. In many cases in which an examination of the imaginal venation fails to disclose a definite 3A, the corresponding trachea may still be found in the pupal wing, thus proving that the reduction is a specialisation from a more archaic condition in which 3A occurred. In some of the higher Planipenna, both the anal tracheæ and veins are much reduced; and it is necessary to make a very careful examination of the freshly-turned pupal wings *in situ*, in order to determine the limits of the three anal veins.

The most archaic condition for these three veins is that in which all three run free, and well separated from one another, and 1A is also separated from Cu_2 above it. The third anal can always be recognised, in archaic forms, from the fact that, if it is simple, then it bounds the area of the jugal lobe in the forewing externally; but, if it is a forked vein, then its posterior branch occupies the same position.

Specialisations of these veins occur by the approach of one towards another, not far from the base of the wing to form typical Y-veins of the type described in Sections iii., vi., as being formed between M and Cu. Text-fig. 51 shows the formation of (a) an incomplete Y-vein, by partial fusion of two veins near



Text-Fig. 51.

Diagrams to show the formation of *a*, incomplete cubito-anal Y-vein in hindwing, and *b*, complete anal Y-vein, in forewing. Lettering as on p. 535.

their bases, while they again diverge distally, and reach the wing-border far apart, and (b) a complete Y-vein, by complete fusion of the two veins from near their bases onwards as far as the wing-border. Of these formations there are two in which the anal veins play a part, viz. the cubito-anal Y-vein, formed by fusion of 1A with Cu_2 , and the anal Y-vein, formed by fusion of two or more of the anal veins amongst themselves.

The Cubito-Anal Y-vein.

If the vein 1A, which is well separated from Cu_2 basally, approaches it a little further from the base, and fuses with it for a greater or less distance, then a *cubito-anal Y-vein* is formed, the upper arm being the basal piece of Cu_2 , the lower arm the basal piece of 1A, and the main stem the fused portions of these two veins (Text-figs. 36, 51a, Plate xxxiii., fig. 20), which may be indicated by the notation Cu_2+1A .

This formation is an ordinal character for the Mecoptera, Trichoptera and Lepidoptera, *in the hindwing only*. It also occurs in the hindwings of a few Megaloptera, and in both fore and hindwings of some of the higher Planipennia. It also occurs in the forewings of some Diptera (see Text-fig. 50).

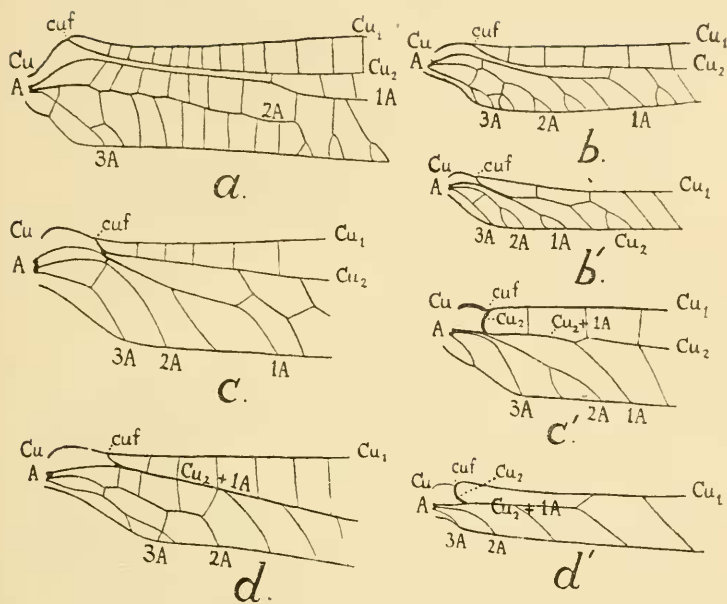
The condition of the cubito-anal Y-vein is generally that of an *incomplete* Y-vein, since the veins Cu_2 and 1A, after fusing for a greater or less distance, diverge again, and run separately to the wing-border. This condition may be studied in Text-figs. 36, 62, 76, 77, 80, 90, and Plate xxxiii., fig. 20. In the Lepidoptera, the formation is as clearly shown in most of the Homoneura as it is in the Trichoptera and Mecoptera. But, in the Heteroneura, it is necessary to study the pupal tracheation, in order to show that a cubito-anal Y-vein does exist. In the pupal hindwing of *Wingia* (Text-fig. 90), I found it absolutely complete; in *Xyleutes* (Text-fig. 87), the fusion was not quite accomplished; and, in many of the higher groups, a secondary specialisation has resulted in the gradual reduction and final extinction of trachea 1A, so that the Y-vein is no longer present. The hindwing of *Carpocapsa* (Text-fig. 89) shows the stage in which the fusion is still present, but 1A is much reduced; while in the Butterflies *Euschemon* and *Euploea* (Text-figs. 99-102) no sign of the Y-vein can be seen.

The best example of this type of specialisation in the Megaloptera is to be seen in *Raphidia* (Text-fig. 107).

In the Planipennia, the approach of 1A towards Cu_2 is first indicated in the *Osmylidae*. In the *Nymphidae* these two veins just touch at a point. In many of the *Myrmeleontidae* the fusion is completed, and the same is true for the *Chrysopidae*, *Apochrysidae* and *Ascalaphidae*. Text-fig. 52 shows the stages in this line of evolution.

The Anal Y-vein.

An anal Y-vein may be formed in different ways, as follows:—(1). In the forewings of all Trichoptera, and of the most archaic Lepidoptera, 2A loops up with 1A, and 3A with 2A, to form a *double anal Y-vein*, or *double anal loop*, as shown in Text-fig. 53a. This formation is confined to these two Orders, for which it is an archetypic character. In the Lepidoptera, the double anal Y-vein may be seen complete in the genera *Sabatinca* and *Mnemonica*, the two most archaic genera of the

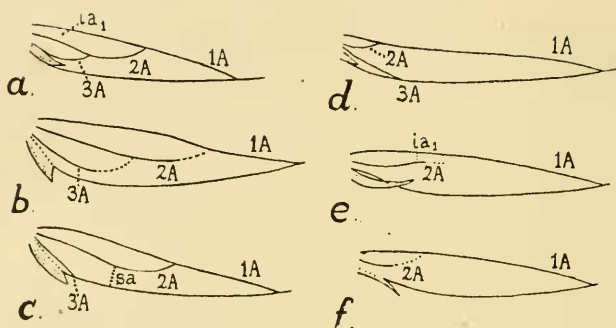


Text-Fig. 52.

Evolution of the cubito-anal Y-vein in the order Planipennia. *a*, unfused condition in forewing of *Osmylus chrysops* (Linn.) (fam. *Osmylidae*); *b*, the same condition in forewing of *Osmyleps placidus* Gerst. (fam. *Myiodactylidae*); *c*, condition of first contact in forewing of *Nymphes myrmeleonides* Leach (fam. *Nymphidae*); *d*, condition of fusion in forewing of *Glenoleon pulchellus* (Rambl.) (fam. *Myrmeleontidae*); *b'*, *c'*, *d'*, the more advanced conditions of fusion in the hindwings of the same insects as in *b*, *c*, *d*, respectively. Lettering as on p. 535.

Jugo-frenata. But, in the other genera of this group, more or less reduction of this formation is generally evident, owing to a progressive weakening of 3A, which results in that vein being unable to maintain its loop intact with 2A. The various stages have been figured already by me in my paper on the *Micropterygidae* (26) and are shown in Text-fig. 53.

It is important to note that, in *Sabatinea* and a number of the Trichoptera, the cross-vein ia_1 persists within the loop



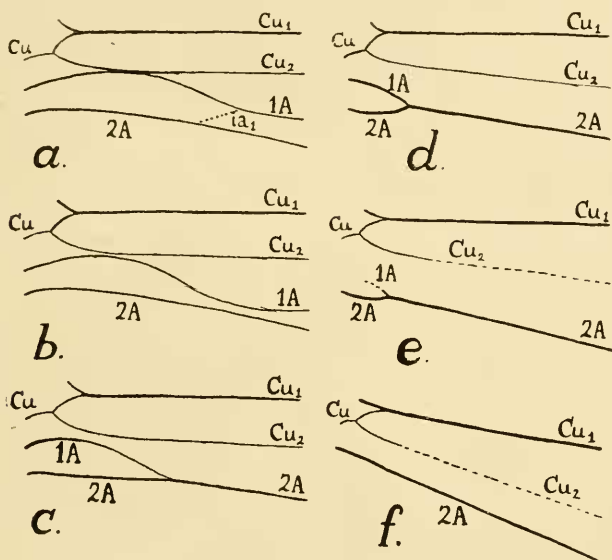
Text-Fig. 53.

Evolution of the anal Y-vein in the forewings of Lepidoptera Homoneura, showing progressive stages of reduction. *a*, original complete double Y-vein formation with inter-anal cross-vein (ia_1) present, in *Sabatinca* (fam. Micropterygidae); *b*, loss of ia_1 , in *Mnemonicia* (fam. Eriocraniidae); *c*, loss of lower loop in *Eriocrania* (fam. Eriocraniidae), (but note presence of sub-anal cross-vein sa); *d*, reduction of upper loop in *Mnesarchaea* (fam. Mnesarchaeidae); *e*, partial loss of upper loop, with retention of ia_1 , in *Trictena* (fam. Hepialidae); *f*, last stage of reduction in upper loop, in *Leto* (fam. Hepialidae). Lettering as on p.535.

formed by 2A and 1A. When we turn to the family Hepialidae, we find a further stage in the reduction of the loop indicated in the genus *Trictena* (Text-figs. 53*e*, 79). Vein 3A has ceased to be chitinised, though its trachea still persists. Further, the distal end of vein 2A has become aborted, and a new connection with 1A is being made via the cross-vein ia_1 . In other genera of this family, the anal veins become still further reduced (Text-fig. 53, *f*) until, in *Charagia* (Text-fig. 78) there is no sign of the original formation left.

In the Heteroneura, the loop formed between 1A and 2A persists in the great majority of forms, including the Butterflies; but 3A is absent from the forewing. The most archaic condition in this Suborder is probably that in which trachea 2A reaches 1A, and the chitinisation of the loop in the imaginal venation is formed around the two tracheae *in situ*. But we may note that, in cases in which 2A is reduced, and does not succeed in quite reaching 1A, a recurrent trachea may grow out downwards and backwards from this vein towards the end of 2A, as

in *Xyleutes* (Text-fig. 85), and the intervening space will still become chitinised in the imaginal venation, thus completing the formation. I have not succeeded in finding the interanal cross-vein ia_1 in any pupa of this Suborder; unless, indeed, the forma-



Text-Fig. 54.

Evolution of the secondary anal Y-vein in the hindwings of the Lepidoptera Heteroneura. *a*, original Homoneurous condition; *b*, condition in pupal wing of *Xyleutes* (fam. *Cossidae*); *c*, condition in pupal wing of *Carpocapsa* (fam. *Tortricidae*); *d*, condition in imaginal wings of the Tortricina; *e*, stage in which the upper arm of the Y-vein (1A) is degrading; *f*, the final stage, in which 2A is left as a straight, simple vein, as in the Butterflies. Lettering as on p. 535.

tion just mentioned in *Xyleutes* indicates that the tracheal outgrowth from 1A proceeds along the channel of that cross-vein. (2) In the hindwings of the older Lepidoptera Heteroneura only, but nowhere else amongst the Orders of the Complex, there is present a remarkable specialisation in the form of an anal Y-vein *secondarily* formed, as the result of the curve given to 1A by the older formation known as the cubito-anal Y-vein,

already dealt with above (p. 577). Text-fig. 54 will explain this formation, which, as far as I am aware, has remained quite unnoticed by all Lepidopterists and students of wing-venation up to the present day. The most archaic stage is to be seen in *Xyleutes* (Text-figs. 54*b*, 87). In this genus, when trachea 1A diverges from Cu_2 , after its approach to it more basally, it converges towards trachea 2A, until they come to lie alongside one another for a short distance about the middle of their lengths. It then diverges again from 2A, but fails to reach the wing border. In the imaginal venation (Text-fig. 88), all that part of 1A lying distad from the fusion with 2A fails to become chitinised. Moreover, the basal portions of the two veins are withdrawn towards the base of the wing, so that the final result is a small basal Y-vein, of much the same type as that seen in the highest stages of evolution of the same Y-vein in the forewing (as in the Butterflies).

An examination of the venation of the Superfamily Tortricina shows that this Y-vein formation is almost universally present in the hindwings of this group. The precedent formation in the pupal wing is well shown in *Carpocapsa* (Text-figs. 54*e*, 89). Here we notice a slight advance upon the condition shown in *Xyleutes*, in that trachea 1A is much shortened, and only just succeeds in reaching 2A after diverging from Cu_2 . But the resulting formation in the imaginal venation (Text-fig. 54, *d*) is practically the same as in *Xyleutes*.

In the Superfamily Tineina, this basal Y-vein of the hindwing is only to be seen in a few archaic genera. In examining the hindwing of *Wingia* (Text-fig. 93) I was just able to make it out as a weakly chitinised formation in the imago. Turning to the pupal tracheation, I was very surprised to find that trachea 1A was well formed and complete, from base to wing-border, and that it maintained its basal contact with Cu_2 intact. There was no sign whatever of trachea 2A, and the course of that vein in the imaginal wing was indicated only by the usual pale band. If this be the usual condition in the Tineina, it indicates a clear dichotomy between them and the Tortricina; for, in the latter, it is trachea 1A which becomes reduced, whereas in *Wingia* the same fate befalls trachea 2A. While further researches are needed on this point, it should be noted that, whereas the Y-vein is retained almost throughout the whole of the Tortricina, it is soon lost in the Tineina, the great ma-

jority of the genera of this group showing no trace of it in the imaginal venation.

This same Y-vein formation may be found at the base of the hindwing in the *Castniidae* (Text-fig. 94) and the *Thyrididae* (Text-fig. 98). It is absent, however, from the higher groups, as, for instance, in the *Psychina*, *Pyralididae* and the Butterflies (Text-figs. 97, 100, 102). An examination of the pupal tracheation in this last group shows that, as in the case of the *Tortricina*, it must have been the trachea 1A which became aborted. For the only trachea left of the two is placed well apart from Cu_2 , and shows no tendency to approach it near the base. Thus we reach the unexpected result that, in the Butterflies, and probably also in the other highly specialised groups, the reduction of the number of anal veins has *not* been by loss of 3A, as hitherto supposed, but by loss of 1A. It should be noted also that, in all these higher groups, although trachea Cu_2 persists in the pupal wing, no chitination is formed around it; and so vein Cu_2 is also absent. Thus the only veins lying below the basal cell in the hindwing are 2A and 3A.

We see, then, that the rise and fall of the anal Y-vein of the hindwing is a line of evolution entirely confined to the Heteroneura. Its origin is most certainly to be traced back to a form in which the approach of 1A to 2A took place at the point where these two veins were joined by the cross-vein ia_1 , as in the Trichoptera and *Jugofrenata* (Text-fig. 54a). This cross-vein must have gradually become shortened, and finally aborted, leaving the two veins in contact. The whole series of evolutionary forms is indicated in Text-fig. 54.

In concluding this account of the anal group of veins, I should like to call attention to the fact that it appears to be only an assumption on Comstock's part that the three so-called anal veins are really three separate veins, each of them equivalent to one of the other more anterior main veins. In the Odonata, there is only one anal vein, which gives off a number of branches, *all of which are convex*. In the Orthoptera and *Perlaria*, 2A and 3A come off from the same stem, though 1A is slightly separated from them. In the Cicada, of which I have examined the tracheation in the wings of several freshly-turned nymphs *in situ*, the anal group of veins comes off from a common stalk in the forewing, as in Odonata, and in the hindwing the con-

dition is that seen in the Orthoptera. I know of no pupal wings in which the three anal veins lie widely separated upon the alar trunk trachea. Even in the Planipennia and Lepidoptera, where they are certainly separate, they lie close together upon this trunk, and are easily distinguished as a separate group. Considering how greatly all the tracheæ are *split back* in the Lepidoptera, even R and M often appearing to arise as two distinct tracheæ from the alar trunk, it would surely seem more logical to take as the more archaic condition that in which the three tracheæ arose from a single base upon the alar trunk, a condition from which all the above described states could easily be derived.

It seems necessary to emphasise this, since otherwise it is hard to understand why the three anal veins should form an exception to the usual rule of alternate convex and concave veins. The fact that they are all three convex certainly points strongly to their being all branches of a single anal vein.

It should be noted that I do not consider Comstock's 1A in Homoptera to be that vein, any more than it is in Lepidoptera. It is certainly Cu_2 , and the cubitus is three-branched in both these Orders. The Y-vein on the clavus of the Fulgoroidea is strictly homologous with the anal Y-vein of the Lepidoptera, and is formed by the looping-up of 2A on to 1A.

Section vi. THE DISTAL Y-VEIN, TRIGAMMA, BASAL CELL AND AREOLE IN THE LEPIDOPTERA.

(Plate xxxiv., fig. 21, Plate xxxv., fig. 23, and Text-figs. 55-59.)

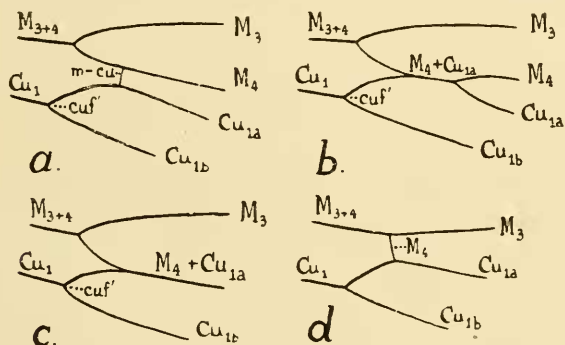
When this research was begun, in 1916, it was recognised that one of the most interesting problems to be studied was the evolution of the Lepidopterous type of wing. At that time, the fossil *Archipanorpa* was known, but *Belmontia* had not been discovered. I saw, then, in the Protomecopterous type of wing-venation, the ancestral form from which the Lepidopterous type could best be derived; and I published a short Preliminary Report (13) in which this idea was followed out. Since then, the discovery of *Belmontia*, and the large amount of time that I have given to researches upon the Lepidoptera, have convinced me that it is the Paramecoptera which are the true ancestral Order from which the Lepidoptera have been derived (29).

The pupal tracheation and imaginal venation of various archaic Lepidoptera have been very fully studied, and the results are given in detail in Section xiv. In this Section, I propose to examine the formation of the distal Y-vein, its evolution into the Trigamma (13), and the stages of the evolution of the basal cell and areole within the Order.

The Distal Y-vein.

I suggest this name for the distal fusion between M_4 and Cu_{1a} which is shown in the *Hepialidae*, and which is a specialisation closely parallel with that called the cubito-medial Y-vein between M_5 and Cu_1 , nearer to the base of the wing.*

The original condition of M_4 and Cu_{1a} must obviously have been that in which they both ran separately to the wing-border;



Text-Fig. 55.

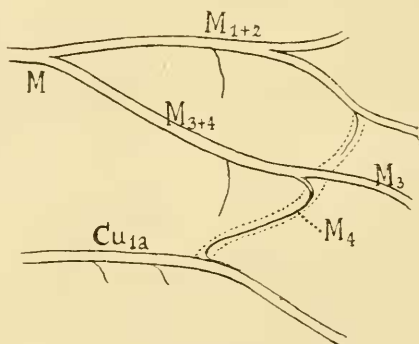
Evolution of the distal Y-vein in Lepidoptera. *a*, the original condition found in the Trichoptera; *b*, the stage of partial fusion, as in hind-wing of *Sthenopsis* and in the fossil *Archipanorpa* (see Text-fig. 57); *c*, formation of the Y-vein completed, as in *Hepialidae* generally; *d*, reduction of M_4 to the transverse position, as in many Lepidoptera. The final stages are shown in Text-fig. 59, *b*, *c*, *d*, where M_4 becomes aligned with basal piece of Cu_{1a} . Lettering as on p. 535.

as they still do, for instance, in the forewings of all archaic Trichoptera (Text-fig. 55*a*). This is followed by an incomplete fusion, in which the two veins are united for a space, and then

*In this connection, the "Note on the Evidence concerning the Existence of Vein M_4 in the Lepidoptera," on p. 651, should be read carefully.

diverge to run separately to the wing-border (Text-fig. 55*b*). This condition is the one found in the hindwing of the well-known atavistic individual of *Sthenopsis* figured by Comstock (15, fig. 337), and also seen in the fossil *Archipanorpa* (Text-fig. 57). Further specialisation results in the formation of the complete distal Y-vein, in which the two veins, after fusing, remain in this condition right to the wing-border (Text-fig. 55, *c*). This stage is the one visible throughout the family *Hepialidae*.

In examining the pupal wing of *Eriocrania*, no trace of a separate trachea M_4 could be found (27). I therefore made very careful examinations of this area of the pupal wing in the *Hepialidae* and *Cossidae*. The result of a large number of dissections proves that trachea M_4 is *never present* in the



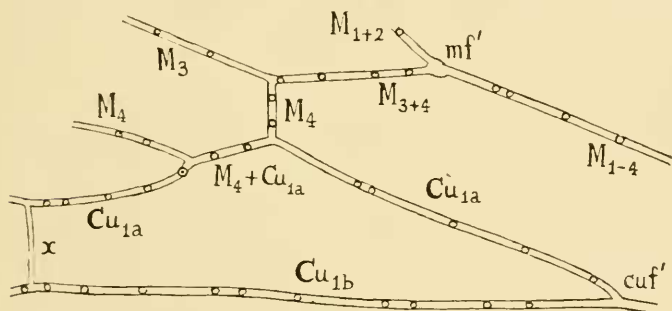
Text-Fig. 56.

Detail from the pupal wing of *Xyleutes* (fam. *Cossidae*), to show trachea M_4 *in situ*. (x 8).

freshly-turned pupal wing of the *Hepialidae*, though I have succeeded in finding it once (Text-fig. 56) in the freshly-turned pupal wing of the Cossid genus *Xyleutes*. In this case, trachea M_4 was small, but quite distinct, and was bent back in the manner shown in Text-fig. 56, in correlation with the highly specialised direction of vein M_4 in the imaginal wing.

In a single pupal wing of *Hepialus* which he examined, MacGillivray (16) also failed to find any trace of trachea M_4 . It would be easy to jump to the conclusion that the vein M_4 has been lost altogether in this family, and that the oblique vein

forming the upper arm of the distal Y-vein is only a cross-vein*. But a little consideration will show that the case is exactly on a level with that of the cubito-median Y-vein, in which M_5 was originally considered to be only a cross-vein, until the discovery of the fossil *Belmontia* proved it to be a main vein. In the fossil *Archipanorpa* (Text-fig. 57), the vein M_4 descends at right angles from the median cell, and would naturally be taken for a cross-vein, were it not for its very strong formation, and



Text-Fig.57.

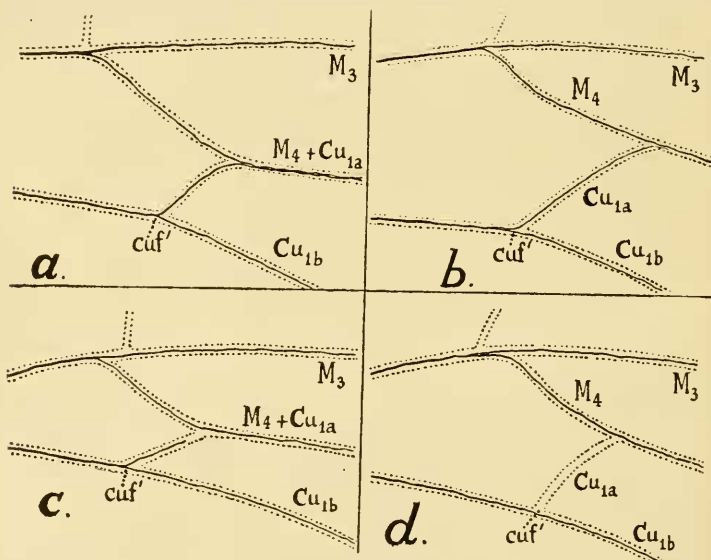
Portion of the hindwing of the fossil *Archipanorpa* (Order Protomecoptera) to show the partial fusion of M_4 with Cu_{1a} , and the transverse position of the former vein. The small circles indicate the positions of the macrotrichial sockets. Note their absence from the true cross-vein x . Lettering as on p.535. (x 10.)

the very evident sockets of the macrotrichia which are still preserved upon it. Thus M_4 in this fossil shows an even more advanced condition than that seen in the *Heptalidae*, as regards its direction; and yet there can be no doubt that it is a main vein.

Having examined the pupal wings of a number of *Heptaliidae*, at various stages of development, and still failing to find any signs of trachea M_4 , it occurred to me that it might very probably develop at metamorphosis, in the same manner as trachea M_5 . For this purpose, I obtained a large number of freshly emerged imagines of *Heptaliidae*, from which I prepared cleared mounts of the wings. The result showed that, although, in the majority of cases, trachea M_4 is not present, yet there were a considerable number of specimens in which it was present. In

*See the Note on this point on p.652.

one genus, *Perissectis*, of which a large supply was available, it was found that the majority of wings showed M_4 present. Moreover, specimens were found, in all the genera examined, in which all stages of the reduction of this trachea were to be seen. A few specimens were also found in which trachea M_4 persisted at the expense of trachea Cu_{1a} , the latter finally becoming aborted. The condition in which both tracheæ were



Text-Fig. 53.

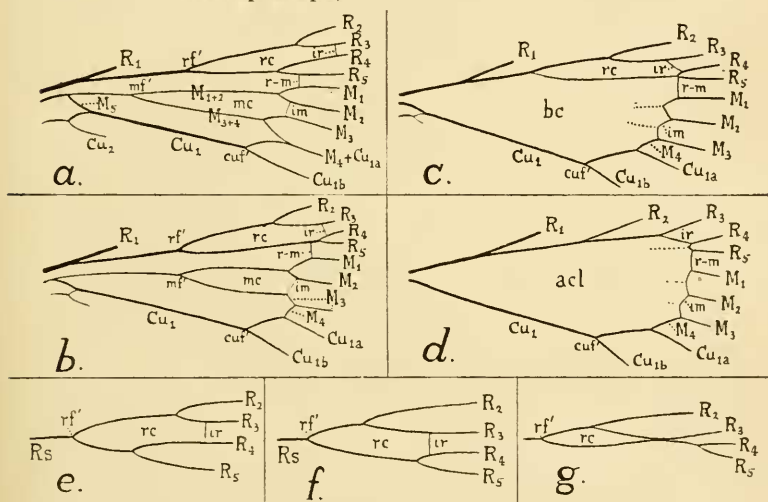
Condition of the tracheation in the imaginal wings of *Hepialidae*, in the region of the distal Y-vein. *a*, both trachea M_4 and trachea Cu_{1a} complete, in *Perissectis australasiae* Don; *b*, trachea Cu_{1a} becoming reduced, in *Charagia splendens* Scott; *c*, further reduction, in *Pielus* sp.; *d*, complete loss of trachea Cu_{1a} , in *Charagia astathes* Turn. Lettering as on p. 535.

well developed is shown in Text-fig. 58, *a*, while the stages in the reduction of trachea Cu_{1a} are illustrated in Text-figs. 58, *b-d*.

An examination of the imaginal venation shows that, in a number of specimens, the chitinisation of the vein M_4 is stronger than that of Cu_{1a} though the reverse is usually the case. This suggests that in the earliest Lepidoptera, vein M_4 was well developed, but was tending to become weakened by its fusion

with Cu_{1a} . The genera in which vein M_4 is most frequently strongly chitinated are also those genera in which trachea M_4 is most frequently present in the imaginal wing, viz. *Perisectis*, *Trictena* and *Pielus*. No pupæ of any of these three genera have yet been obtained; but I shall continue to make every effort to get them, in the hope that trachea M_4 may appear in the pupal wing.

Taking into consideration the above evidence, coupled with the very evident examples of incomplete fusion in *Sthenopsis* and the fossil *Archipanorpa*, we are, I think, justified in a belief



Text-Fig. 59.

Evolution of the basal cell and areole in Lepidoptera. *a*, original condition, as in Trichoptera (and in *Hepialidae*, except for loss of *ir*); *b*, change to the Heteroneurous condition, as in forewing of some *Cossidae* (note the approach of the forking of R_{2+3} towards rf'); *c*, formation of the open basal cell (*bc*) by abortion of M_{1-4} and its branches, as far as *im*, as in most Heteroneura; *d*, formation of an areocel (*acl*), by fusion of the areole (*rc*) with the basal cell, through abortion of the chorda (R_{4+5}) as in Tortricina, etc. *e-g*, stages in the evolution of the areole (*rc*); *e*, the Homoneurous condition (*ir* absent in *Hepialidae*); *f*, the Heteroneurous condition, with the forking of R_{2+3} approaching closer to rf' than does that of R_{4+5} ; *g*, closure of the areole by fusion of R_3 with R_{4+5} , after loss of *ir*. Lettering as on p. 535.

that vein M_4 does exist in the Lepidoptera, and forms the upper arm of the distal Y-vein. I think, however, that the notation $M_4 + Cu_{1a}$ need only be applied to the fused vein when it is clear that both M_4 and Cu_{1a} have taken part in the fusion, as in the *Hepialidae*. In the Heteroneura, and also in *Eriocrania*, vein M_4 is reduced to the semblance of a cross-vein. While still labelling this vein M_4 , it does not appear to me that it takes any part in the fusion; and I should prefer to label the distal part of the Y-vein simply Cu_{1a} .

The Trigamma.

Text-fig. 59, *a-d* shows the stages in the alteration of the direction of M_4 which result in that vein becoming aligned more or less with the basal portion of Cu_{1a} , so that the original form of the distal Y-vein is quite lost. The changes are correlated with the development of the *basal cell*, which requires a strong support below it, as well as above. To the strong three-pronged fork formation found in many higher types of Lepidoptera I have already given the name *trigamma* (13). The forks, named from below upwards, are Cu_{1b} , Cu_{1a} and M_3 , the connecting piece between the two last being the highly specialised M_4 , as shown in Text-figs. 59, *c, d*.

The Basal Cell and Areole.

Originally, as in the Trichoptera, there were only two closed cells lying away from the base of the wing in the Lepidoptera. These were the *radial cell* (*re*), formed between R_{2+3} and R_{4+5} , and closed distally by the cross-vein *ir*; and the *median cell* (*mc*), formed between M_{1+2} and M_{3+4} and closed distally by the cross-vein *im*. The primitive condition is shown in Text-fig. 59, *a*. The cross-vein *ir* is retained in the Tortricina and Tineina, as well as in a few other genera, e.g. the Cossid *Macroclyttara* (32). But in most cases it has disappeared, and the closure of the radial cell distally is brought about by other means, such as a partial fusion between R_3 and R_{4+5} (Text-fig. 59, *g*). The cross-vein *im*, on the other hand, is present in most Lepidoptera, and may persist long after the main stem of *M* has become aborted.

The radial cell, when it persists as a separate entity in the imaginal venation of the Lepidoptera, is known as the *areole*. The basal part of the stem of R_{4+5} , which separates the areole,

when present, from the basal cell below it, has been named by Turner the *chorda* (32).

The *basal cell* of the Lepidoptera is formed normally by the abortion of the main stem of M_{1-4} and its two branches M_{1+2} and M_{3+4} , as far as the limits of the median cell distally, i.e. up to the cross-vein *im*. All stages in this reduction are to be met with in existing types, as can be seen by a study of the wing-venations figured in Section xiv. The basal cell, therefore, includes within itself the original median cell, and is separated from the areole above it by the *chorda*. The veins bounding the basal cell distally have been called collectively the *disco-cellulars*. But it is better to retain their correct designations, if we wish to preserve in our minds a true picture of what the basal cell really is. The *disco-cellulars*, from above downwards in order, are the cross-vein *r-m*, the basal piece of M_1 , the basal piece of M_2 , the cross-vein *im*, and a short basal piece of M_{3+4} . Below this, the cell is bounded by the stem of the trigamma.

The basal cell may be enlarged, in the forewing only, by the incorporation within it of the areole or radial cell. This is brought about by the abortion of the *chorda*, or portion of R_{4+5} , separating them. The complete cell so formed has been named by Turner the *areocel* (32). An *areocel* is normally formed in those Tortricina in which no separate areole can be seen, and in many Tineina, as, for example, in *Wingia* (Text-figs. 90-93). An *areocel* of a somewhat specialised type is also formed in the Butterflies, as may be seen from the account given in Section xiv., pp. 679-687. It differs from the *areocel* of the Tortricina in that, before it was evolved, the radial sector has become split into two parts R_{2+3} and R_{4+5} , arising separately from R_1 , and wide apart. In Text-fig. 59, I have indicated the more important stages in the evolution of the basal cell and areole, culminating in the formation of the highly specialised *areocel*.

In the hindwings of Heteroneura, the formation of an *areocel* is not possible, owing to the reduction of Rs to a simple, unbranched vein. Thus there is never an areole present in this wing, and the most complete formation of the basal cell is that formed by the loss of M_{1-4} and its two main branches, as far as the cross-vein *im*, by the alignment of the *disco-cellulars*, and by the strong formation of the trigamma. This type of cell is to be found in all the higher groups, quite independently of whether the forewing possesses an *areocel* or not.

Section vii. VEINLETS AND CROSS-VEINS.

The distinction between a *veinlet* and a *cross-vein* has already been made in Part 2 of this work (25, p. 628). A *veinlet* is a branchlet of a main vein; it is preceded by a trachea in the pupal wing, and carries macrotrichia in all archaic groups. A *cross-vein*, on the other hand, is a transverse vein which is developed independently of the branching system of any main vein; it is not preceded by a trachea in the pupal wing (except in a few cases of high specialisation), nor does it carry macrotrichia in any archaic group.

Veinlets originally come off obliquely from their main veins. But they frequently tend to assume a transverse position, and so come to take on the characters of cross-veins. In the course of reduction, they may lose their precedent tracheæ, or their macrotrichia, or both. In such cases, their true nature is only to be determined by a study of their homologues in more archaic types.

Cross-veins originally formed transverse struts or supports between main veins or their branches. They may, however, become specialised so as to take up an oblique position, and may even become lengthened, so as to appear like veinlets or even branch-veins. In a few highly specialised cases, they may gain an underlying trachea in the late pupal wing, or at metamorphosis. In two groups, viz. in the higher Planipennia and the Raphidioidea, they gain macrotrichia. In such cases as these, their true nature can only be determined by a study of their homologues in more archaic types.

In certain cases, as, for example, when two main veins fuse together for part of their courses, a small portion of a main vein may become bent at an angle to the rest, and so take on the appearance of a veinlet. Further specialisation may cause the trachea underlying this vein to weaken, so that it becomes a veinlet to all intents and purposes. It may even lose its trachea and macrotrichia, and take on a transverse position, so as to be indistinguishable from a true cross-vein, except by a study of its origin in more archaic forms.

Main veins which have undergone these specialisations are the following:—

The basal pieces of M_5 and Cu_1 , during the evolution of the cubito-median Y-vein. (*See* Section iii.).

The basal piece of M_4 in Lepidoptera (Section vi.), or of

M_{3+4} in the higher Planipennia, during the evolution of the distal Y-vein in the former Order, or its homologue, the oblique-vein formation, in the latter.

The only system of true veinlets present in the original Panorpoïd wing is the series of small branchlets from the main veins to the costal border. These may be classed as follows:—

(1) *Costal veinlets*, lying between the costal border and the subcostal vein. These extend from near the base to near the distal end of Sc, running obliquely outwards and upwards from Sc, of which they are true branches.

(2) *Pterostigmatic veinlets*, lying between the costal border and R_1 , distad from the end of Sc. These are branches of R_1 . The evolution of the *pterostigma*, as a hardened patch of membrane covering the area originally supplied by these veinlets, has been already dealt with in Part 2 of this work (25, p. 633).

Besides these original systems of veinlets, there may be developed, as specialisations in the Neuropteroidea only, a series of *terminal veinlets*, formed by the splitting into two of the tips of the veins reaching the wing-border. This splitting may go on almost indefinitely in certain cases, the final result being a long series of veinlets proceeding from quite a considerable portion of the whole length of the vein affected. These extreme cases are only to be found within the Planipennia; and, since they are obvious specialisations, they do not concern us here.

The original system of cross-veins in the Panorpoïd wing, to judge by the fossil evidence, was either one in which the cross-veins were only moderately numerous, very irregularly placed, and very weakly formed, or else they were entirely absent. It will be assumed here that the former was the case, for the reason that it is never possible to be quite sure, in examining a fossil, that such weak cross-veins were not present, even if no visible impression of them has been left. The point is not of much importance, because, even if the Panorpoïd wing was originally without cross-veins, they certainly soon began to appear. In the Permian fossil *Permochorista*, a few can be definitely made out, while traces of others seem to be indicated. In *Belmontia*, they are weakly formed, but all clearly visible in a good light. The main point to be emphasised is this, that the system of abundant cross-veins found in so many forms, e.g. *Merope*, some of the Megaloptera, and most of the Planipennia, is not the original condition, but is a specialisation of much later date,

brought about by the necessity for supporting an abundant main venation by means of numerous transverse struts. A study of the Triassic, Liassic and Jurassic fossil Planipennia proves the truth of this absolutely; while a study of the still existing families of the same Order shows that all the more archaic forms possess only few cross-veins, whereas the higher families show more and more abundant cross-venation, though this is significantly confined only to the *disc*, or middle portion of the wing, and not to the marginal areas. Thus we have the curious result that the Planipennia, which formed a part of the old Order Neuroptera, do not deserve this name at all, as they were originally an open-veined type quite unlike the densely-veined Odonata or Plectoptera, to which the name was much more suitably applied. In other words, Linnæus included, in the one Order, not only those Orders in which the densely-veined condition was the original one, but also those in which it was a high specialisation, only found in the most advanced families. This error has had grave consequences; and, unfortunately, there still remain entomologists who are unable to see the essential differences between the two types, and continue to treat the old Neuroptera as a natural unit.

In determining the Archetypes of the various Orders within the Complex, the conditions of both the system of veinlets and the system of cross-veins must be taken into consideration.

As regards the *veinlets*, the Archetypes may be arranged into four sets showing progressive evolution in this character, as follows:—

(A) Orders in which the more archaic families, and therefore the Archetypes, retain the complete system of veinlets, at any rate as far as the costal series is concerned:— MECOPTERA, PROTOME-COPTERA, PARATRICHOPTERA, MEGALOPTERA and PLANIPENNIA.

(B) Orders in which the costal series is reduced to *three* veinlets only, viz. the humeral (*hm*), the intermediate (*icv*) and the distal (*dv*):— PARAMECOPTERA.

(C) Orders in which the more archaic families, and therefore the Archetypes, possess only *two* veinlets in the costal series, viz. the humeral (*hm*) and the distal (*dv*):—

TRICHOPTERA, LEPIDOPTERA.

(D) Orders in which the more archaic families, and therefore the Archetypes, possess only *one* veinlet in the costal series, viz. the humeral (*hm*):— DIPTERA.

As regards the *cross-veins*, the Archetypes may be arranged into three sets showing progressive evolution, as follows:—

(A) Orders in which the more archaic families, and therefore the Archetypes, show no definite arrangement of the system of cross-veins, which remain weak and irregularly placed in positions of no special mechanical advantage:—

MECOPTERA, MEGALOPTERA, PLANIPENNIA, PARATRICHOPTERA.

(B) Orders in which the cross-veins are reduced in number, and mostly occupy positions of distinct mechanical advantage, but there may still be more than one cross-vein in a set between two main veins:— PARAMECOPTERA, PROTOMECOPTERA, TRICHOPTERA.

(C) Orders in which the more archaic families, and therefore the Archetypes, have the cross-vein system still further reduced, and confined to a few cross-veins, in positions of distinct mechanical advantage, with not more than one cross-vein between any two main veins:—

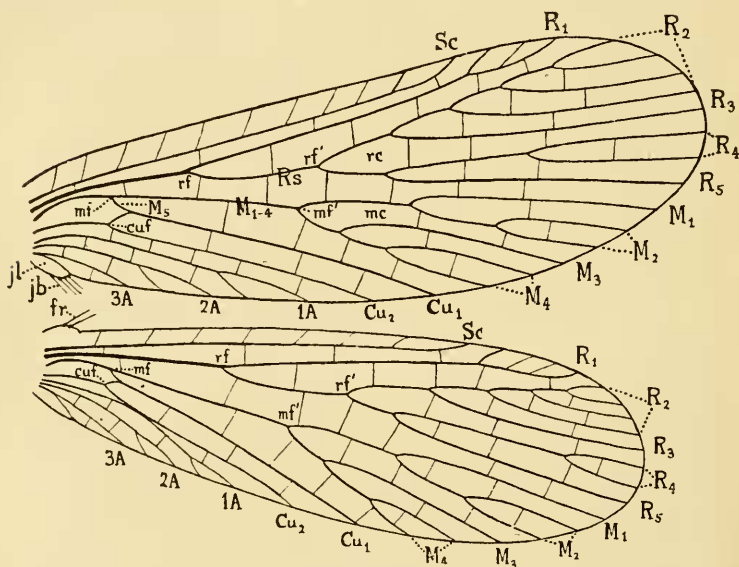
LEPIDOPTERA, DIPTERA.

As regards the *cross-veins*, the most archaic condition is that in which they were either absent or weakly formed, and show no arrangement in positions of mechanical advantage. The Archetype of the Mecoptera appears to have possessed this condition, which is indicated by A in Table v. on p. 706. In the Megaloptera and Planipennia, a slight degree of specialisation is evident, in so far as there are three cross-veins placed in advantageous positions between R_1 and R_s , two between Sc and R_1 , and the rest appear to show some signs of arrangement to mechanical advantage. The Protomecoptera and Paratrichoptera also show slight signs of specialisation in the arrangement of their cross-veins. I have therefore classed these four Orders as slightly specialised under B in the Table mentioned. The Paramecoptera, with an evidently more specialised system of cross-veins (Text-fig. 63) are placed under C. Of the more reduced systems, that of the Archetype of the Trichoptera contains more cross-veins than that of the Lepidoptera, and that of the latter more than that of the Diptera. These may therefore be arranged in ascending order of specialisation, under the letters D, E, F, respectively, in Table v. on p. 706. Complete lists of the cross-veins present in the Archetypes of the Orders Trichoptera, Lepidoptera and Diptera will be found under the Sections dealing with the venations of these three Orders.

Section viii. THE VENATION OF THE MECOPTERA.

(Text-figs. 60-62.)

Text-fig. 60 shows a diagrammatic representation of the wings of the Archetype of this very ancient Order. In constructing this Archetype, the following points have had to be borne in mind:—



Text-Fig. 60.

Wings of the Archetype of the Order Mecoptera. Lettering as on p.535.

(1) In most of the existing genera, the cross-vein system is fairly strongly developed, and usually has the effect of causing a slight zig-zagging of the main veins. In the fossil genera, the cross-vein system is very weakly developed, and, in the oldest genera, there is practically no deviation, due to cross-vein struts, in the courses of the main veins. This is well shown both by the Permian genus *Permochorista* (6) and the Triassic *Mesochorista* (20), as well as by most of the Liassic forms. Consequently the typical zig-zagging of the main veins seen in many recent genera is omitted from the Archetype. The system of dotted cross-veins given in Text-fig. 60 is intended to represent

an entirely irregular and variable system of very weakly chitinised cross-veins, such as can just be made out with difficulty in the oldest fossils, and is not to be taken as indicating that there were any cross-veins fixed in constant positions. Indeed, I would go so far as to express the opinion that Permian forms may yet be discovered in which no cross-veins exist at all, beyond a few in specially suitable positions, e.g. as supports beneath the dichotomous forkings of R_s and M_{1-4} .

(2) Though the cubito-median Y-vein disappeared very early from the wings of this Order, by fusion of Cu_1 with M_{1-4} near its origin, yet this formation is indicated in the pupal wing of *Chorista* (23), and is present, fully formed, in the Triassic fossil *Stereochorista*. It is therefore included in the Archetype. I am also of opinion that Permian forms will be discovered showing this Y-vein as complete as it is in *Stereochorista*, and thus serving to link the Paramecoptera with the true Mecoptera.

(3) The cubitus is two-branched throughout the Order, the fork being close to the base of the wing. Cu_1 is a strong, straight, convex vein without any distal forking. Cu_2 is a weak, concave vein, lying in or near the anal furrow.

(4) A single line of descent is clearly evident, with very little change during many millions of years, from the Permian genus *Permochorista*, through the Triassic *Mesochorista*, to the still existing *Taeniochorista*, with *Chorista* itself as a specialised offshoot. Apart from the changes already indicated in (1) above, the only alteration of importance is the reduction in the number of dichotomie branches of M_{1-4} in the recent genera, which have only five such branches in the forewing, and four in the hind. In the fossil genera, this vein has six branches, all of which are clearly primitive dichotomies. Thus the Archetype of the Order must also have at least six true dichotomie branches of M_{1-4} , as in Text-fig. 60. The manner by which reduction has been brought about is quite evident. The first fork to be eliminated was that of M_4 , the result being the condition now extant in the forewings of *Taeniochorista* and *Chorista*. Further reduction, in the hindwings only, led to the loss of the fork of M_2 . This condition of a four-branched M_{1-4} persists in all recent winged forms within the Order.

(5) As contrasted with the Australian *Choristidae*, the forms known from the Northern Hemisphere show a progressive reduction not only in the number of dichotomie branches of M_{1-4}

(from six to four), but also in those of Rs, which, in all known *Choristid* forms, from the Permian onwards, only number four. Thus we find in *Merope* either five or six dichotomic branches of M_{1-4} , and always five such branches of Rs. The only specimen of this rare insect which I possess, and from which Text-fig. 61 was drawn, has five branches of M_{1-4} in all four wings; but the specimen figured by Comstock (15, fig. 317) has six on the right side, the extra one being due to a strong dichotomy of M_{4b} . As it seems doubtful whether this extra fork may not be a recent addition due to platygenesis, I have not counted it as an archetypic character.

As regards Rs, the extra fork in *Merope* occurs on R_2 , and is so deep that there can be no doubt of its being a primitive dichotomy. The same fork persists throughout the genus *Panorpa*. But, in the archaic genus *Panorpodes* there is to be found a deep forking of R_4 which is also clearly archaic. Thus the northern forms at present existing must have had an ancestor with at least a six-branched Rs, the extra forks being present on R_2 and R_4 respectively.

Further valuable evidence on this point is to be gained by the study of the Liassic genus *Orthophlebia* (2, Pl. xlii.) and allies. Many of these show Rs with no less than *seven* branches, while the rest have six. In this group of fossils, the extra branches all belong to R_2 , and tend to be arranged pectinately,—a very striking illustration of how very simple a change might lead to the evolution of the Neuropteroid type of venation, from the older Panorpoïd type. Allowing *five* branches as the maximum for R_{2+3} , as in the *Orthophlebiidae*, and *three* for R_{4+5} , as in *Panorpodes*, we see that the Archetype of the Order must have possessed at least *eight* branches to Rs, as shown in Text-fig. 60.

It will by now be clearly evident that the main line of evolution within the Mecoptera has been by *narrowing* of the wings, with suppression of certain of the original archaic branches of Rs and M_{1-4} . With the narrowing there has proceeded also a *lengthening* process, which culminates in such forms as the *Bittacidae*. Thus the name Mecoptera ("long-winged insects") is fully justified for this ancient Order.

(6) In all Mecoptera, and therefore in the Archetype of the Order, Sc is shorter in the hindwing than in the fore, and Cu_2 is fused with 1A for part of its length, not far from the base,

in the hindwing only. These characters are included in Text-fig. 60, and serve to show that Handlirsch's assertion that this Order has retained "archaic homonomous wings" is the result of too cursory a survey of the venational characters.

(7) The apex of the wing is well rounded in all forms throughout the Order.

(8) The pupal wings are merotracheate, as in the archaic *Choristidae* (23).

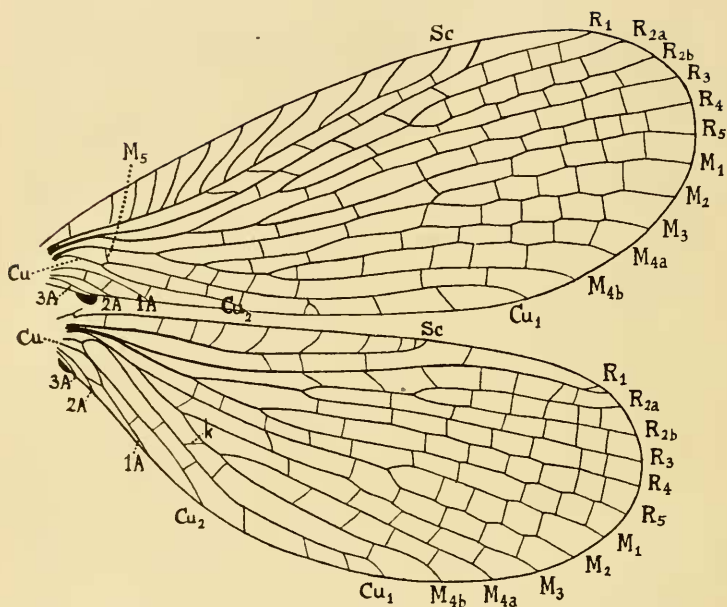
Having now indicated the principal characters of the Archetype of this Order, and the methods by which they have been arrived at, it will only be necessary to give a fuller study of the aberrant but archaic genus *Merope*, the venation of which has been very seriously misinterpreted by Comstock, and to tabulate the principal characters of the known families of the Order.

The Venation of the genus Merope.

In working out the Archetype of the Mecoptera, much weight has to be given to the evidence offered by this genus. Comstock (15, fig. 317) has interpreted its venation along the lines of his hypothetical type, in which the number of branches of Rs and M_{1-4} respectively is limited to four. I have made a careful study of a female specimen of this rare insect, in my own collection, received in exchange from Mr. Nathan Banks, to whom my best thanks are due. As a result, I am quite unable to agree with Comstock.

Text-fig. 61 shows the venation of this insect, and Text-fig. 62 the bases of the two wings, much enlarged. The points in dispute are the limits of M and Cu. The vein which I call M_{4b} , and which, in Comstock's specimen, is strongly forked in both wings, is labelled by him Cu_1 ; and an ingenious, but quite unsound, argument is used to explain away the obvious fact of its attachment to M. This explanation involves the veins lying below these two, and is best given in Comstock's own words (15, p. 304):—

"In the forewing of the specimen taken at Ithaca, cubitus and the first anal vein coalesce for a short distance. Immediately after vein Cu separates from 1st A, Cu_1 extends transversely to the long axis of the wing and anastomoses with vein M for a considerable distance. . . . The anal furrow is along the first anal vein. . . . In the hindwing of this specimen vein Cu_1 anastomoses with vein M_4 for a short distance."



Text-Fig. 61.

Wings of *Merope tuber* Newm. (x 63). Lettering as on p. 535. *k*, cross-vein taken by Comstock to be the basal piece of Cu_1 .

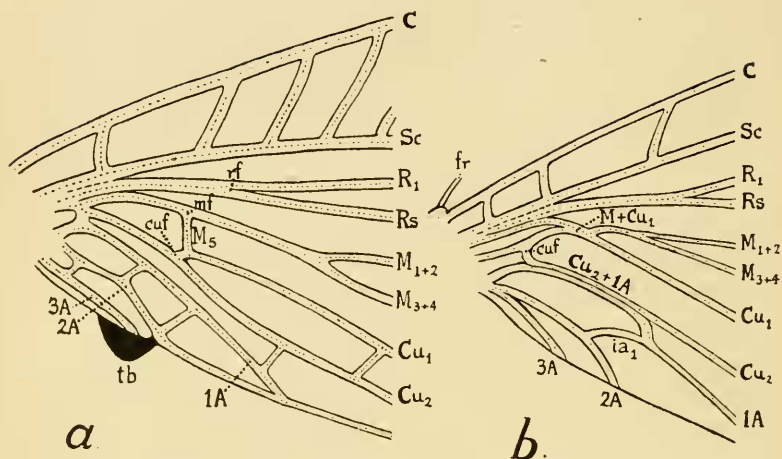
The above explanation is made clear in Comstock's figure by his labelling of the cross-vein which I have marked *k*, in the hindwing, (Text-fig. 61) as Cu_1 . The cross-vein in the same position in the forewing is left unlabelled by him; but the wording leaves us without any doubt that this same cross-vein is intended to be taken as Cu_1 in the forewing also, and is the means whereby this vein has become fused with M.

Now, in all Mecoptera, it is the vein Cu_2 (always a very concave vein) which lies along the anal furrow. Also, except in the highly specialised *Bittacidae* and *Nannochoristidae*, the fusion of Cu_1 with M for a short distance is confined to the hindwings. It would be very remarkable if such an admittedly archaic type as *Merope* were to be highly specialised in these two characters. Thus I doubted from the first the correctness of Comstock's diagnosis, and was led to study the genus more carefully myself.

In fixing the homologies of the veins in *Merope*, I had recourse first of all to the trichiation. *Merope*, like all archaic types throughout the Complex (25), has macrotrichia upon the main veins only, and not upon the cross-veins. It was thus a very simple matter to prove that the cross-vein which I have marked *k* (Text-fig. 61), and which Comstock considered to be the basal piece of Cu_1 leading to its fusion with *M*, was in truth a cross-vein, and not a portion of a main vein. Neither this cross-vein, nor any other cross-vein near it, carries any macrotrichia at all in *Merope*. Having settled this point, I searched for the true cubital fork, and found it easily enough quite close to the base of the wing, as shown in Text-fig. 62. The position of this fork is indicated by Comstock (15, p. 304) by the words "Immediately after *Cu* separates from 1st *A*," which imply a basal fusion of *Cu* with 1*A*. Such a fusion does not exist. The two veins are, of course, Cu_1 and Cu_2 , and their point of separation is the cubital fork *cuf*. Further, in the forewing, a strong bar falling very close up to this fork indicates the position of M_5 , which is here present, but in the transverse stage already indicated as present in many Trichoptera (Section iii.). There is no fusion whatever between *Cu* and 1*A* in the forewing; and the three anal veins are all present, though 3*A* is much reduced, and was not noticed by Comstock.

It will be seen that the condition of the venation at the bases of the wings of *Merope* is the normal condition for the Order, except only that the basal part of the wings is much narrowed, and the three anal veins much reduced in consequence. *All the basal or primary dichotomies are present, very close to the base;* and the specialisations found in the hindwing, viz. the fusion of Cu_1 with M_{1-4} for a short distance, and the fusion of Cu_2 with 1*A* for a longer distance, are exactly paralleled in other genera. In the specimen which I examined, the fusion of Cu_2 with 1*A* in the hindwing was actually clearly shown by the presence of a line dividing the two fused veins, as shown in Text-fig. 62; so that there could be no doubt whatever as to the correct homologies of these two veins.

Since, then, the boundaries of 1*A* and *Cu* are those indicated in Text-figs. 61, 62, it is abundantly clear that M_{1-4} in *Merope*, as in the forewing of *Chorista* and allies, has more than four branches. In my specimen, these branches agree exactly with



Text-Fig. 62.

Basal portions of *a*, forewing, and *b*, hindwing of *Merope tuber* Newm., enlarged, to show the true courses of M and Cu. (x 20). Lettering as on p. 535. Note the presence of M₅ in forewing, and the fusions of M with Cu₁, and Cu₂ with 1A, in hindwing.

those of *Chorista* forewing. In Comstock's specimen, M_{tb} had an extra fork on the right side only. As this fork is only a small one, and as *Merope* is clearly a type specialised by broadening of the distal portion of the wings (in contrast with the rest of Mecoptera) I have not counted this fork in as an archetypic character, although its presence in Comstock's specimen might easily be claimed as an archaic survival.

In conclusion, it is clear that *Merope* is an archaic type, in so far that it still retains more than four branches of both R_s and M₁₋₄, thus combining the leading characters of the *Panorpidae* and *Choristidae*. But it is specialised along a line of its own, by the intense narrowing of the basal portions of the wings, by the broadening of the distal portions, by the widening of the costal area, and consequent alteration of the form of the costal veinlets, by the increase and density in the cross-venation, and by the formation of the peculiar tubercle at the base of the forewing. It is, in fact, a Scorpion-fly evolving into a cockroach-like type, resting with its wings nearly flat, instead of held in a high roof-like manner, and probably much given to hiding

away in crevices or under stones, where this type of specialisation would be of value for concealment. The working out of the life-histories of this remarkable insect, and its ally *Notiothauma* should certainly be undertaken by those living where these insects occur, and may be confidently expected to add much to our knowledge of the Mecoptera.

TABLE OF THE PRINCIPAL VENATIONAL CHARACTERS FOR THE
FAMILIES OF THE ORDER MECOPTERA (TABLE i.).

In presenting this Table, I have had to divide the Order into a number of distinct families, some of which have not so far been definitely recognised. The *Choristidae* will include the genera *Taeniochorista* and *Chorista*, confined to Australia, and distinguished from the *Panorpidae* (s. str.) by many good characters, one of which is the presence of a five-branched media in the forewing, and the presence of only four branches to Rs in both wings. I have already defined the *Permochoristidae* (6). But I cannot find any good distinctions between the Triassic *Mesochorista* and the Permian *Permochorista*, and am convinced that these two genera must be placed in the same family. Consequently the family name must be changed to *Mesochoristidae*, since that genus was defined first (20). The characters of the *Orthophlebiidae* have already been defined by Handlirsch (2, p. 479), and those of the *Stereochoristidae* (28) and *Nannochoristidae** by myself. The *Meropidae* may be made to include provisionally *Notiothauma* as well as *Merope*, though the venation of the former has not yet been thoroughly worked out on modern lines. The *Bittacidae* are a very distinct group, with very definite wing-characters; while the *Boreidae*, being wingless, are omitted from the Table.

In the Table, the archaic condition of any given character is indicated by the letter A, while more specialised conditions are indicated by B, C, . . . in ascending order. The Archetype of the Order is the type which possesses the condition A for *all* characters. The percentage of archetypic characters possessed by the most archaic representative of each family is shown in the bottom line of the Table, and affords an interesting comparison of the relative archaism of the different families, as far as their wing-venation only is concerned.

*These Proceedings, xlii., part 2, 1917, pp.284-301.

TABLE I. (MECOPTERA).

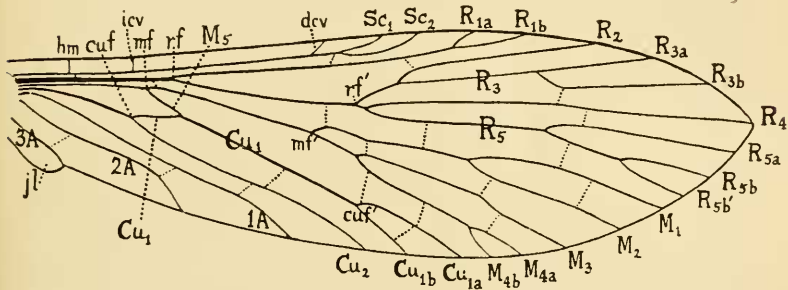
| Ref. No. | Character. | <i>Mesochoristidae</i> (Permian and Trias) | <i>Stereochoristidae</i> (Trias) | <i>Choristidae</i> (Recent) | <i>Nannochoristidae</i> (Recent) | <i>Orthophlebiidae</i> (Lias and Jura) | <i>Meropidae</i> (Recent) | <i>Panorpidae</i> (s. str.) (Recent) | <i>Bittacidae</i> (Recent) |
|----------|--|---|-------------------------------------|--------------------------------|-------------------------------------|---|------------------------------|--|-------------------------------|
| (1) | Number of branches of Rs.—A. More than four. B. Four. C. Only three. | B. | B. | B. | C. | A. | A. | A. | B. |
| (2) | Number of branches of M ₁₋₄ . — A. More than four. B. Four. | A. | A. | Fw.A. Hw.B. | B. | A or B. | A. | B. | B. |
| (3) | Branches of Cu.—A. Two, with Cu ₁ complete. B. Two, with Cu ₁ cut short. | A. | B. | A. | A. | A. | A. | A. | A. |
| (4) | Condition of M ₅ . — A. Complete, as in <i>Belmontia</i> . B. Reduced to transverse vein in forewing, absent in hind. C. Lost in both wings. | C. | A. | B or C. | C. | C. | B. | B. | C. |
| (5) | Fusion of Cu ₂ with 1A in hindwing.—A. Present. | A. | [A.] | A. | A. | A. | A. | A. | A. |
| (6) | Condition of costal veinlets.—A. Full series. B. Greatly reduced. | A or B. | ? | A or B. | B. | B. | A. | B. | B. |
| (7) | Condition of cross-venation.—A. Absent, or very weak and irregular. B. Strongly developed, but irregular. C. Regular, reduced to a few in special positions. | A. | A. | A or B. | C. | A. | B. | A or B. | B. |
| (8) | Shape of wings.—A. Normal, with well rounded tip; anal veins not reduced. B. Narrow base and broad distal portion; anal veins reduced. C. Wing much narrowed and elongated, with petiolate base; anal veins reduced. | A. | A. | A. | A. | A. | B. | A. | C. |
| | Percentage of archaic characters present in most archaic member of each family:— | 75.0 | 71.4 | 68.8 | 37.5 | 75.0 | 62.5 | 62.5 | 25.0 |

Section ix. THE VENATION OF THE PARAMECOPTERA.

(Plate xxxi., figs. 15, 16, and Text-fig. 63.)

This Order is only represented at present by a single genus, *Belmontia*, from the Upper Permian of Belmont, near Newcastle, N.S.W. Text-fig. 63 shows the restored forewing of this insect. The actual specimen has about 0.5 mm. of the extreme base, including the jugal lobe, missing, and a small piece of the tip of the wing broken off obliquely. There is, therefore, no difficulty in completing the venation with certainty.

As this fossil has already been fully described by me in a



Text-Fig. 63.

Forewing of *Belmontia mitchelli* Till. (Order Paramecoptera, Upper Permian), restored. (x 5) Lettering as on p. 535. Note the complete cubito-median Y-vein.

former paper (29), it will only be necessary here to refer to that work, and to indicate the principal points in which *Belmontia* differs from the true Mecoptera, as well as those in which it is of importance in indicating the lines of descent of some of the still existing Orders of the Complex.

Belmontia differs from all true Mecoptera in the following points:—

- (1) Cu_1 is forked distally into Cu_{1a} and Cu_{1b} .
- (2) The forking of R_{4+5} takes place exceedingly close to the origin of that vein.
- (3) The cross-vein system is reduced to a definite plan, which resembles fairly closely that of the Trichoptera, Lepidoptera and Diptera, though still possessing a number of cross-veins not found in these Orders.

Besides these points, when I founded the Order Paramecoptera, I emphasised the presence of the complete and beautifully formed cubito-median Y-vein, which is unique in its perfection. The only known Mecopteron in which this Y-vein is present is the Upper Triassic *Stereochorista*, which I was, therefore inclined to regard as exceptional for that Order. However, as will now be seen from Section iii., a more complete comparative study of this formation makes it almost certain that this Y-vein was present in all the Orders of the Complex originally. Hence the character may no longer be used for separating the Paramecoptera from the Mecoptera, and one of the principal differences between the two Orders breaks down. I think it can only be a matter of time before other new fossil types, either from the Permian of Newcastle or from the Trias of Ipswich, will be discovered, in which this Y-vein will be found perfectly formed, though perhaps not quite so prominently as in *Belmontia*.* Ultimately it will, no doubt, be possible to show a series of forms making a complete connection between *Belmontia* and the true Mecoptera; so that the Paramecoptera may then be merged into the Mecoptera as a separate Suborder. The same will undoubtedly prove to be the case with the Protomecoptera of the Ipswich Trias, dealt with in the next Section, since these are even more like the true Mecoptera than *Belmontia* is.

Another distinction to be noted, of less importance, is that the wing of *Belmontia* was almost certainly more or less pointed, whereas the wings of all true Mecoptera, even those of the very slender-winged *Bittacidae*, are always well rounded at the tips.

The points that are of importance in *Belmontia*, as regards the evolution of the more recent Orders, are as follows:—

(1) *The cubito-median Y-vein.* This is fully dealt with under Section iii.

(2) *The distal forking of Cu₁.* Whether this fork originated from an incomplete fusion of M₅ and Cu₁ distally, or not, it is quite certain that the forked condition is more archaic than the simple straight condition found in the true Mecoptera, the Paratrachoptera, and the Diptera. The forked condition is retained in the Trichoptera, Lepidoptera, Megaloptera and the

*Since this was written, Mr. Mitchell has forwarded me a new Mecopteron from the Upper Permian of Belmont, N.S.W., in which the cubito-median Y-vein is well formed. R. J. T.

Planipennia. This question will be found discussed under Section iv.

(3) *The peculiar situation of the forking of R_{4+5} .* A little movement of this fork basad would bring it to the main stem of Rs. From this position, R_4 could then become detached from R_5 , and begin to migrate along the upper branch of Rs, viz. R_{2+3} . A discussion of the origin of pectinate forking of Rs will be found under Sections ii., xv., and xvi.

(4) *The number of branches of Rs and M_{1-4} .* The branches of these veins in this very archaic type are clearly original dichotomies, not additions to an originally simpler venational scheme. Thus the fact that *Belmontia* possesses more than four branches to both is a serious blow to Comstock's original hypothetical type, and prevents us from accepting such a type, with its four-branched Rs and M_{1-4} as in any way representing the ancestral venational type for the Complex. This conclusion is most strongly supported by the condition of Rs and M_{1-4} in the Protomecoptera (Section x.), as well as in the great majority of the known fossil Mecoptera and Planipennia. The question is fully dealt with under Section ii.

The great value of the discovery of the fossil *Belmontia* lies principally in its affording a definite proof of the presence of the extra basal posterior branch of M, viz. M_5 , fused with Cu_1 to form the cubito-median Y-vein, and also in disclosing to us a type from which the Trichoptera and Lepidoptera can most certainly be derived, by way of a common stem-form not yet found in the fossil state, but which must have existed somewhere in Triassic times, though not necessarily in Australia. It also tends to show the Mecoptera in their true form, viz. as a somewhat isolated and very early specialisation from the original stem-form of the Complex, and not in any way to be considered as the ancestral Order from which any of the still existing Orders have sprung.

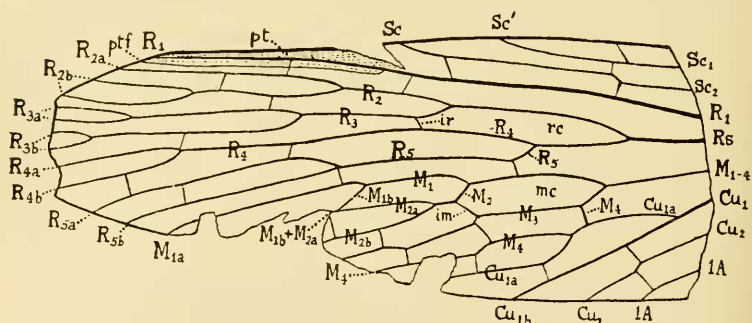
Section x. THE VENATION OF THE PROTOMECOPTERA.

(Text-figs. 57, 64.)

The Order Protomecoptera (5) was founded by me for the reception of the remarkable Upper Triassic fossil *Archipanorpa magnifica* Till., from Ipswich, Q. A large portion of both the fore and the hind wings of this fine insect is preserved. As

I have already described the venation very fully, and figured both wings, together with a restoration, it will only be necessary here to correct an error in my original description, and to emphasise those points which mark this type as distinct from both the true Mecoptera and the Paramecoptera.

Text-fig. 64 shows the preserved portion of the hindwing of this fossil. In my original description (5, p. 188 et seq.) I indicated the presence of a true costal vein, distinct from the anterior margin of the wing, and made this one of the ordinal characters. A further examination of this vein shows me that, like the subcosta below it, it is distinctly a *concave* vein. Now I think that there can be no doubt that a true costal vein, if it were to occur in any insect, would be a *convex* vein; seeing that



narrower pterostigma (*pt*) of the hindwing, in the absence of the distal forking of R_{3a} in the forewing, and in the fact that M_{1b} and M_2 do not fuse to form a Y-vein in the forewing, as they do in the hind. The wonderful preservation of the archediectyon, and of the sockets of the macrotrichia in this fossil has already been emphasised (5, 25); but I think it is necessary here to draw attention again to the fact that the distribution of the macrotrichia upon the veins has been made use of in determining the courses of the main veins. It would not have been possible to determine the correct course of M_4 without these structures, since the basal piece of that vein, though much more strongly formed than any cross-vein present, is bent at right angles to M_3 , and would undoubtedly have been considered a cross-vein, if it were not for the presence of large macrotrichia upon it (Text-fig. 57). Also, the inter-median cross-vein (*im*), closing the median cell (*mc*) distally, is bent obliquely, and might easily have been mistaken for a piece of a main vein, were it not for its very weak formation, and the absence of macrotrichia upon it.

It is most unfortunate that we do not know what the basal parts of the wings of this fossil were like. With our present knowledge of *Belmontia* to guide us, it would seem to be extremely probable that the cubito-median Y-vein was present, fully formed. In this respect my original restoration would need to be corrected (5, Pl. ix.).

In a comparison of this fossil with *Belmontia*, it should be noted that, besides being much the larger insect, *Archipanorpa* has the larger number of branches of Rs, viz. ten in the forewing, as against seven in *Belmontia*. Further, it is quite clear that *Archipanorpa* is undergoing stenogenesis, seeing that M_4 and Cu_{1a} are already partially fused in both wings, and M_{1b} with M_{2a} in the hind, not to mention the very obvious crowding of the distal branches together. All the branches of Rs in this fossil are clearly original archaic dichotomies, as they are also in *Belmontia*; there can be no question of the addition of extra branches from the tip backwards, in either form. Thus we have to accept *Archipanorpa* as less reduced and more archaic than *Belmontia*, as regards the condition of its radial sector, in spite of the fact that it is an Upper Triassic form, while *Belmontia* is Upper Permian.

The most crushed together of the branches of Rs in *Archip-*

panorpa are the distal forkings of R_2 and R_3 . Elimination of all the branches of R_4 , and all but the most basal of R_3 , would give us the condition found in *Belmontia*. R_4 only forks once in *Archipanorpa*; the loss of this fork would give the unforked condition of this vein seen in *Belmontia*. The latter genus, however, has the more archaic R_5 , with three branches, as against the two present in *Archipanorpa*; and this difference shows that reduction is not proceeding on the same lines in these two forms.

As regards the media, M_1 and M_2 are both forked in *Archipanorpa*, simple in *Belmontia*; while M_4 is simple in the former, but forked in the latter. So that, both as regards Rs and as regards M, *Belmontia* tends to keep the more posteriorly placed forks, *Archipanorpa* the more anteriorly placed ones.

Archipanorpa is more specialised than *Belmontia* in that it already possesses a partial fusion between M_4 and Cu_{1a} , on the same lines as that found in the well-known aberrant hind-wing of the genus *Sthenopsis* of the family *Hepialidae* (15, fig. 337), and therefore indicating the method by which the present completely fused condition of these two veins has been brought about in the Lepidoptera (Section vi.). Further, M_4 has already attained the transverse position in this fossil,—a fact which makes it much easier to understand the condition of this vein in almost all Lepidoptera to-day. This evolution of M_4 in the Lepidoptera and in the fossil *Archipanorpa* is an excellent example of that *parallel development* which is so frequently noticeable in widely separated types which have sprung from the same stem, and have therefore inherited the same tendencies.

In both *Belmontia* and *Archipanorpa*, it is Cu_{1b} which continues the line of the main stem of Cu_1 distad, while Cu_{1a} arches up away from this line, towards M_4 . The condition is of interest, as showing the strong tendency there must have been, from the very first, as soon as stenogenesis set in, for at least a partial fusion of these two veins to take place; or, failing that, for Cu_{1a} to be eliminated entirely, leaving the strong, straight Cu_1 that is so typical of the Mecoptera, Paratrachoptera and Diptera.

It does not seem possible to compare very closely the vein Sc in *Archipanorpa* and *Belmontia*, seeing that we do not know how far back towards the base the dichotomy of this vein took place in the former. All we can say for certain is that *Archipanorpa* exhibits the more archaic condition, and that the sub-

costa was evidently a strongly forked vein in the Archetype of the Complex.

Section xi. THE VENATION OF THE PARATRICHOPTERA.

(Text-fig. 65.)

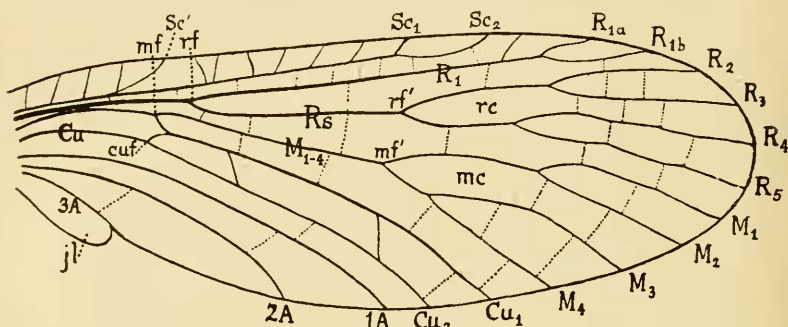
In this Order I have recently placed four remarkable genera from the Upper Trias of Ipswich, Q., viz. *Mesopsyche*, *Triassopsyche*, *Aristopsyche*, and *Neuropsychyche*, described by me in two previous papers (5, 28). At first sight these wings appear to belong to the Trichoptera; but a closer analysis shows that they do not belong to that Order at all, and are much more closely related to the Mecoptera and Diptera.

To these four genera I now wish to add the genus *Mesopanorpodes*, originally described by me under the name *Mesopanorpa*, from the Wianamatta Shale of Glenlee, N.S.W., and probably of very much the same age as the Ipswich fossils (6, pp. 746-7). The name *Mesopanorpa* being preoccupied, I changed it to *Mesopanorpodes*.* Originally, I considered this fossil to be an aberrant member of the Order Mecoptera. But it is now apparent that it will go best into the Paratrachoptera, with which it agrees in every particular, except for the possession of a somewhat larger number of cross-veins than are to be found in the Ipswich genera. We may note especially the presence of two cross-veins in this genus between R_2 and R_3 , as in *Neuropsychyche*, and between R_4 and R_5 , as in *Mesopsyche*. The base of the wing appears to be more narrowed in *Mesopanorpodes* than it is in any of the Ipswich genera. Both in this respect, and in possessing the submedian cross-vein (*sm*) present also in *Protoplasia* (Text-fig. 67), amongst the Diptera, *Mesopanorpodes* is perhaps the nearest Paratrachopterous type yet discovered to the true Diptera.

The archetypic forewing of the Order Paratrachoptera, as shown in Text-fig. 65, has been constructed by selecting all the most archaic characters exhibited by the five genera already named, and incorporating them into one wing-type. The most complete wings are those of *Aristopsyche* (28, p. 202), and *Mesopanorpodes* (6, p. 746); these genera have, therefore, played the greatest part in the formation of the Archetype. *Aristopsyche* is the only genus of the five in which a basal branch of

*These Proceedings, xliii., pt. 3, 1918, p.435.

Sc is preserved, as shown in the Archetype. As in the case of the Protomecoptera, I took this branch originally for a true costal vein. Further study of the fossil has, however, convinced



Text-Fig. 65.

Forewing of the Archetype of the Order Paratrachoptera. Lettering as on p. 535.

me that it is a true branch of Sc, since it is evidently a concave vein, and its attachment to Sc can actually be made out in the fossil itself.

The cross-vein system is most abundant in *Mesopanorpodes*, *Mesopsyche* and *Neuropsyche*. The zig-zagging of the veins R_4 and R_5 in *Mesopsyche* (5, Pl. vii., fig. 1), caused by the incidence of the two cross-veins already mentioned above, is a specialisation, and is not to be found in *Mesopanorpodes*, which possesses the same two cross-veins. It is, therefore, omitted from the Archetype, which is made to resemble *Mesopanorpodes* in the nearly straight condition of these two veins. But this latter genus is specialised in having the forking of R_{4+5} placed more distally than that of R_{2+3} ; so that the Archetype must be made to agree with the other four genera in this respect. All the cross-veins shown in Text-fig. 65 are to be found in one or other of the five genera comprising the Order Paratrachoptera.

It is quite impossible, at present, to say what is the significance of the two strong oblique veins descending from Cu_1 . They are not present in *Mesopanorpodes*, *Mesopsyche* or *Neuropsyche*; but both are preserved intact in *Aristopsyche*, and the more distal one is also clearly to be seen in *Triassopsyche*. As there is no sign of the sockets of the macrotrichia upon these

very delicate wings, it is impossible to say definitely whether these veins are specialised oblique cross-veins, or really descending branches of Cu_1 which fuse with Cu_2 . Their evident strength would incline one to the latter belief. But the decision must stand over for the present; and I will content myself with calling attention to their existence, without taking them into consideration at all in the construction of the Archetype of the Complex. If further discoveries should prove that they are true branches of Cu_1 , then it is clear that that vein must originally have had more branches than we at present suppose; and the Archetype of the Complex must be altered accordingly.

The Archetype of the Paratrachoptera clearly agrees with the usual definition of the venation of the Order Mecoptera in many points. It seems inevitable that, sooner or later, the discovery of intermediate forms, either in the Permian or Trias, must link the two together, and cause us to merge the Order Paratrachoptera into the Mecoptera, with the rank of a Suborder. No Mecopteron is yet known with a basal branch of Sc present, as in *Aristopsyche*; so that, in this character, the Archetype of the Paratrachoptera is more archaic than that of the Mecoptera. The cubito-median Y-vein is not clearly preserved in any of the four known genera, but appears to have been lost by fusion of Cu_1 with M_{1-4} in *Aristopsyche*, as far as this part of the wing can be made out. However, we have already seen how this structure turns up in the more archaic forms of other Orders of the Complex (Section iii.). Hence I have included it in the Archetype characters, with the firm belief that further fossil finds in this Order will show that it was present.

The Paratrachoptera are specialised from the original Mecopterous type by their distinctly Trichopterous facies, which is most marked in the shortening of the apical forks belonging to Rs and M_{1-4} , and the consequent formation of the radial and median cells (*rc*, *mc*), and the veins arising from them, on strictly Trichopterous lines. As regards the median cell, it should be borne in mind that the Diptera also share this character with the Trichoptera; and there can be no doubt that this was also the case with the radial cell in the Diptera, before specialisation set in and removed one of the four branches of Rs. As regards the cubitus, the Paratrachoptera differ strongly from the Trichoptera, but agree with the Mecoptera and Diptera, in having Cu^1 running straight to the wing-border, without any

distal forking. They also agree with the Mecoptera in the generalised condition of the anal area of the forewing. This character marks them off most strongly from the Trichoptera, in which the three anal veins form a double Y-vein, and from the Diptera, in which the anal area is narrowed, and the anal veins much reduced.

It will be clear from the above evidence that the Paratrachoptera must be regarded as a somewhat specialised side-branch from the old Mecopterous stem, and that they arose at a time when the basal branch of Sc, preserved in *Aristopsyche*, had not been entirely eliminated from the venation. Since this branch of Sc has not yet been noticed in any true fossil Mecoptera, although a much more complete branch is present in the Triassic Protomecoptera (Section x.), we should probably be on very safe grounds in assuming that the Paratrachoptera, like the Protomecoptera, must have already become differentiated in Upper Permian times. Thus, representatives of the Order may confidently be expected to be found, when more complete investigations of the beds of this age, in Australia and elsewhere, can be carried out.

The great importance of the Paratrachoptera as an Order is that they do most certainly indicate the line of descent of the Diptera from ancient Mecopterous-like forms. A comparison of the Archetypes of the two Orders Paratrachoptera and Diptera will be made in the next Section, and will clearly show how simple a derivation of the Diptera from this Triassic Order can be proved, as far as the venation of the forewing is concerned.

Section xii. THE VENATION OF THE DIPTERA.

(Text-figs. 43, 48-50, 66-70.)

The determination of the venation of the Archetype of this huge Order is a matter of little difficulty, in spite of the immense number and variation of the venational types existing within it at the present day. As the pupal wings are merotracheate,—and, indeed, little is known about them at all in comparison with the pupal wings of the dominant holotracheate Order Lepidoptera,—I have not been able to attempt a complete analysis of the venational types of the various archaic families within the Order, as I have done in Section xiv. for the Lepidoptera. Such an attempt, in the case of the Diptera, would

only resolve itself into a study of the comparative morphology of the imaginal venation, and would scarcely be productive of any new evidence concerning the Archetype, or the Phylogeny of the Order as a whole; though it would, no doubt, help considerably in elucidating the phylogeny of the various groups and families within the Order itself.

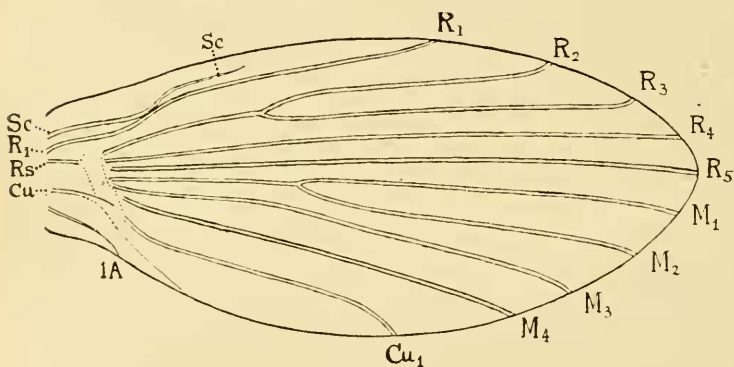
In constructing the Archetype of this Order, the question of outstanding importance is the determination of the correct limits of veins M and Cu . I have dealt with this under Section iv. The archaic *Rhyphus* (Text-figs. 48, 68b) may be taken as the test genus, although the same result will be obtained from any other genus in which the macrotrichia are sufficiently well preserved, as in many of the older *Tipulidae*, *Leptidae*, etc. The result of a study of *Rhyphus*, or any of these latter forms, on the lines indicated in Section iv., is to prove conclusively that Cu_1 is a simple, unbranched vein, as in the Mecoptera and Paratrachoptera, and that M_{1-4} is four-branched, the vein M_4 being the one which Comstock (15, fig. 357 et seq.) has labelled Cu_1 , while the true Cu_1 is the vein which he has labelled Cu_2 . The true cross-vein *m-cu* is devoid of macrotrichia, and connects the two veins M_4 and Cu_1 , just distad from the origin of the former in *Rhyphus*. The vein labelled *m-cu* by Comstock is the basal piece of M_4 as it arises from the median cell, and carries strong macrotrichia in *Rhyphus* and other archaic genera. The difference between the condition of Cu_1 in the Diptera, and the condition of the same vein in archaic Trichoptera and Lepidoptera, where it carries a strong distal fork, has not been sufficiently appreciated hitherto, and is most strongly emphasised here.

In working back to the archetypic venation of this Order, it is at once apparent that we may leave out of account not only all the Cyclorrhapha, which are highly specialised, but also the numerous groups, both in the Nemocera and the Brachycera, in which the venation shows definite reduction, or specialisation by fusion of the distal branches of the main veins. We are thus left with the *Tipulidae* (s. lat.) and *Psychodidae* amongst the Nemocera, the *Rhyphidae*, *Leptidae* (s. lat.), *Stratiomyiidae*, *Therevidae*, *Tabanidae*, *Asilidae* and allies amongst the Brachycera.

The *Psychodidae* are evidently a very archaic group, but specialised by reduction, and by the loss of almost all the original connections between the main veins. At the base of the wings

in this family, chitinisation is very weak, so that the connections of the main veins cannot be made out with certainty. It is clear, however, that R_s retains the four-branched condition in *Psychoda* (Text-fig. 66), while, in those genera in which one branch has been lost, the forking of R_{2+3} is still retained, as in other archaic *Nemocera*. The limits of M and Cu are not determinable with certainty. But the probability is that M_{1-4} has remained four-branched, as in *Rhyphus*, while both Cu and the anal veins have been greatly reduced, by the narrowing of the base of the wing. The labelling of the veins in *Psychoda*, given in Text-fig. 66, assumes this to be the case.

In the *Tipulidae* (s. lat.) there are many archaic types still



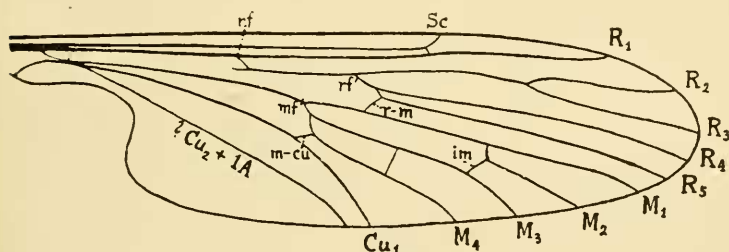
Text-Fig. 66.

Forewing of *Psychoda* sp. (fam. *Psychodidae*, Gosford, N.S.W.).
(x 36). Lettering as on p. 535.

existing, though all are specialised by the extreme stenogenesis, which has strongly affected the basal parts of the wings. Text-fig. 49 shows the venation of the Australian genus *Gynoplistia*, in which the median cell (*mc*) is very nicely preserved, with M_4 coming off from it in such a manner as to leave not a shadow of a doubt as to the correct interpretation of that vein. In this genus, as in almost all *Nemocera*, R_s has been reduced by the elimination of the fork of R_{4+5} , while R_2 and R_3 still exist as separate veins. As R_{4+5} usually forks, in all archaic types within the Complex, much closer to the main stem of R_s than does R_{2+3} , it does not seem at all likely that this reduction has been carried out by the removal of this fork distad, until it be-

came lost at the apex. A much stronger probability is that either R_4 or R_5 has been *entirely* suppressed, by lack of chitinisation, as in the case of Cu_2 , and occasionally also M_2 , in a number of Lepidoptera. Pending a full proof of what has happened, I have labelled the unforked part of Rs, R_{4+5} .

The genus *Protoplasa* (Text-fig. 67) is remarkable in still possessing the four branches of Rs, though R_5 appears somewhat crowded in between R_4 and M_1 . The evidence of this genus, then, reinforces that of *Psychoda* as to the original four-branched condition of Rs in the Diptera; and this condition will therefore be adopted for the Archetype. *Protoplasa* also has an extra cross-vein connecting M_3 with M_4 , which is strongly suggestive of an original Mecopterous or Paratracheopterous condition, in which the apical forks were supplied with such excess cross-veins.



Text-Fig. 67.

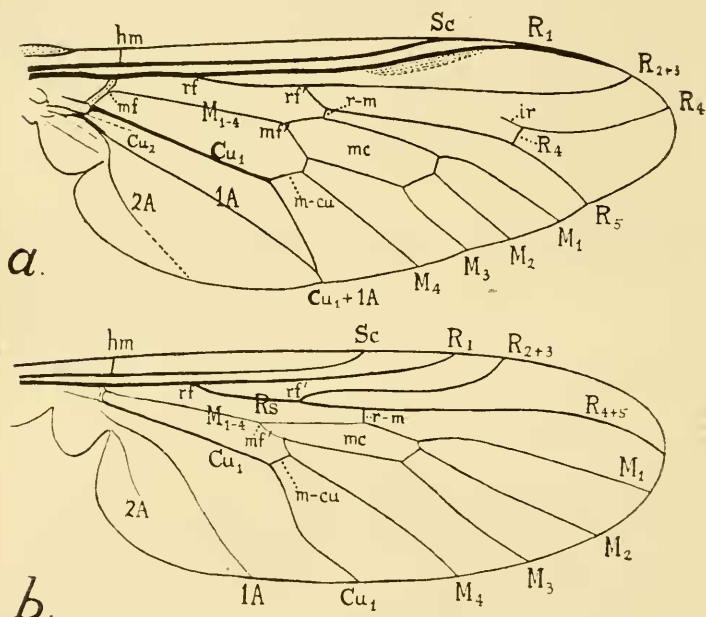
Forewing of *Protoplasa fitchii* (fam. *Tipulidae*) after Comstock, but with lettering altered. Lettering as on p. 535.

Some light is thrown upon the condition of the anal part of the wing in Diptera by a study of the *Tipulidae*. In *Gynoplistia* (Text-fig. 49) there is a clearly marked remnant of Cu_2 , most strongly chitinised basally, and fused with 1A (a much more strongly marked vein), for some distance beyond the cubital fork (*cuf*). Vein 2A is well developed, and is connected with 1A near its base by the inter-anal cross-vein.

Turning next to the Brachycera, we may select *Tabanus* and *Rhyphus* (Text-fig. 68) as representing two of the most archaic wing-types for this Sub-order, though many other genera of the families mentioned above, on p. 615, would do equally well. The points to be noted are:—the reduction of Rs to a three-branched condition, by means of the elimination of the fork of

R_{2+3} (contrast with this the line of evolution in the Nemocera); the archaic condition of the median cell (*mc*) with the four branches of M_{1-4} normally situated with regard to it; and the presence of the cross-veins *r-m*, *im* and *m-cu*, as well as the lower portion of *ir*, in the form of a stump-vein. The humeral veinlet (*hm*) is also present.

The line of evolution within the Brachycera leads to a number



Text-Fig. 68.

Forewings of *a*, *Tabanus circumdatus* Walk. (fam. *Tabanidae*). (x 8), and *b*, *Rhyphus brevis* Walk. (fam. *Rhyphidae*). (x 15). Lettering as on p. 535. Note the condition of M_4 and Cu_1 . (See also Text-fig. 48).

of venational types in which a reduction is brought about by the formation of Y-veins of the type already noted in Sections iii., v., vi., but in this Order affecting all the distal branches of the main veins. The Y-vein is formed by fusion of two veins distally, and may be brought about only after much altera-

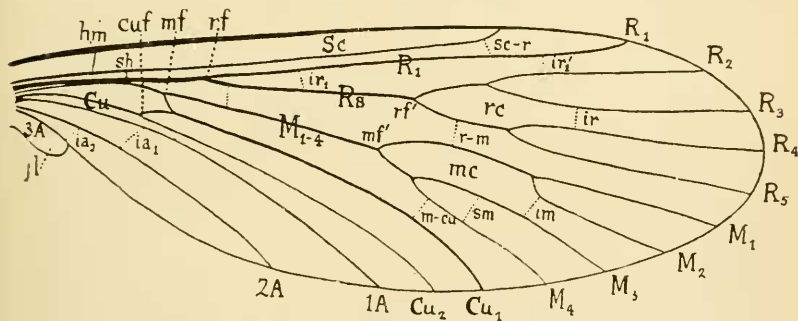
tion in the original courses of the veins involved. All stages of this line of evolution can be followed out within the single family *Bombyliidae*; but its details need not be gone into here.

The probable condition of the cubito-median Y-vein in the oldest Diptera has already been discussed in Section iii. It is only here necessary to refer to Text-fig. 43 for justification of the assumption that this formation did exist in the Archetype of the Diptera, though probably already in a somewhat reduced condition.

The Archetype of the Order, as constructed on the evidence given above, will have the forewing venation as given in Text-fig. 69. The following characters should be noted:—

(1) Both Sc and R_1 are simple, unbranched veins; and the only costal veinlet present is the humeral (hm).

(2) Both Rs and M_{1-4} have four branches. The radial cell



Text-Fig. 69.

Forewing of the Archetype of the Order Diptera. Lettering as on p. 535.

(rc) is present, and is closed distally by ir , since this vein is indicated by a short stump-vein arising from R_4 in many *Tabanidae* (Text-fig. 68). The median cell (mc) is also present, and closed by im .

(3) The cubito-median Y-vein was present, though probably already in a somewhat reduced form.

(4) Cu_2 was weakly chitinised, and perhaps already obsolescent.

(5) The base of the wing had already become somewhat narrowed; and, as a result, $1A$ must have been very close up to Cu

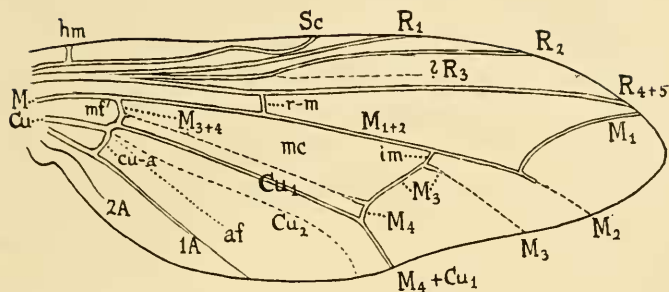
basally. As this vein is fused with Cu_2 in some *Tipulidae*, but with the main stem of Cu in *Stratiomyiidae*, I have left it just free in the Archetype, so as to allow the fusion to take place independently in either position, according to the line of evolution followed.

(6) Vein 3A is, at the most, only present as a very short, weakly chitinated vein bounding the jugal lobe distally.

(7) The cross-vein system is much reduced, and consists of the following only:—the subhumeral (*sh*); the subcosto-radial (*sc-r*); the inter-radial between R_1 and R_2 (*ir'*) present in many *Tipulidae*; the inter-radial (*ir*) closing the radial cell; the radio-median (*r-m*); the intermedian (*im*) closing the median cell; the submedian (*sm*) from M_3 to M_4 (found only in *Protoplasa*); the medio-cubital (*cu-m*); and the first inter-anal (*ia_1*)

A comparison of this Archetype with that of the Paratrachoptera shows us at once that the Diptera can be directly derived from this fossil Order by reduction. A narrowing of the wing-base, with consequent reduction in the anal veins, and approach of 1A to Cu ; reduction of Sc' to the humeral veinlet; loss of all the other costal veinlets and the distal forkings of Sc and R_1 ; some reduction, probably, in the condition of the cubito-median Y-vein; and, finally, a considerable reduction in the cross-vein system; these changes would produce the archetypic Dipterous forewing from that of the Paratrachoptera. As far as the hindwings are concerned, we have to assume for the Archetype of the Diptera that they were already evolved into well-formed halteres. All the known wings of the Paratrachoptera being almost certainly forewings, we cannot say for certain what the state of the hindwings was in that Order. But it is clear, in any case, that the Diptera are descended from some originally four-winged type, although the intermediate stages of the process are not known to us.

In connection with the Order Diptera, and probably also in the case of the two other Orders, Mecoptera and Trichoptera, in which the pupal wings are merotrichate, I desire here to emphasise the value of a careful study of the imaginal wing, *during and just after expansion*, when the fly emerges from the puparium. My attention was first called to this when I happened to examine the expanding wings of a number of undetermined species of *Tachinidae*, whose puparia I had placed in a



Text-Fig. 70.

Forewing of an undetermined Tachinid ($\times 5$) immediately after full expansion. Lettering as on p.535. For full explanation see text.

glass jar. Text-fig. 70 shows the state of the imaginal venation in the freshly expanded wing of this fly. Quite a number of veins were strongly indicated, at this stage, which were seen to disappear again not very long afterwards, when the wing became hardened up. We may mention the following:—

(1) What appeared to be an incipient attempt at redeveloping R^3 was visible as a very slight band arising from R_2 in the position shown, but not reaching the wing border. If this were really R_3 , it must indicate an attempt to reproduce a very archaic stage, since the forking of R_{2+3} has been lost in all Brachycera, and therefore, presumably, in the ancestors of the Cyclorrhapha.

(2) M_2 was clearly visible as a distinct band right up to the wing-border. As soon as the wing had hardened up, the only chitinisation left of this vein was the short stump-vein indicated by the continuous black line arising from M_1 in Text-figure 70.

(3) The course of M_{3+4} was clearly marked as a weak band arising from mf' , and running parallel to, and a little above, Cu_1 . This vein divided distally into M_3 , running up obliquely to meet the cross-vein im , and then bending again to run longitudinally to the wing-border, and into M_4 , which turns at right-angles to M_{3+4} as a short transverse vein and joins Cu_1 immediately below its point of origin. Besides these formations, M_{3+4} was connected, just distad from mf' , by the cross-vein $m-cu$, to Cu_1 . As the wing hardened up, all the main stem of

M_{3+4} became rapidly obliterated, leaving only the short basal connection from mf' to $m-cu$, and a short distal stump-vein projecting inwards from the point of origin of M_3 and M_4 . Also, the distal free piece of M_3 became rapidly obliterated, leaving only a short stump attached to im , and closely resembling the stump of M_2 above it. Naturally, I expected that these stumps would remain, when the wing had become quite hardened up. But I was surprised to find that both the outwardly projecting stump of M_3 , and the inwardly projecting stump of M_{3+4} , became finally eliminated, leaving a single unbroken and only slightly waved vein connecting Cu_1 below with M_{1+2} above. Comstock (15, p. 356) has, naturally enough, taken this vein to be the inter-median cross-vein (m of his notation, im of mine); whereas it is now seen to be a *composite vein*, made up of a short piece, im , above, a long piece of M_3 in the middle, and a short piece of M_4 below. Another change in the hardened wing was the straightening out of the basal stump of M_{3+4} , together with the cross-vein $m-cu$, to form a single strong transverse brace-vein, which might well be named the *secondary arculus*, seeing that it plays the part of bracing the wing in the same region as the original arculus does in older types. Care must be taken to distinguish the two formations, as there is no trace left of the original cubito-median Y-vein in the Myioidaria.

(4) The course of Cu_2 , and the line of the anal furrow (af) running below it, are visible in the freshly expanded wing, but are obliterated later. $1A$, part of $2A$, and the cross-vein $cu-a$ remain chitinised in the hardened wing.

The above evidence seems to me to be of very great value, as indicating a new method of studying the venation of highly specialised types of Diptera. In particular, I think that every occurrence of *stump-veins* ought to be noted down, and attempts made to find out what their condition is in the freshly expanded imaginal wing. In this connection I will now only refer to the stump-vein arising from R_4 in many *Tabanidae* (Text-fig. 68). I have taken this as the remnant of the inter-radial cross-vein ir , which is its most obvious interpretation. But I hope that any entomologist, who may have the opportunity, will examine the freshly formed wing of any suitable species, to see what other formations may be indicated there (as, for instance, the possible presence of a separate R_3).

It should be noted here that there is a very great difference

between the most archaic types of the Cyclorrhapha, such as the *Syrphidae*, and the Myiodaria. The former have the original arculus, or cubito-median Y-vein, strongly formed near the base of the wing; while the secondary arculus, formed from the base of M_{3+4} and the cross-vein *m-cu*, is only just beginning to move basad, and is little altered from its normal position as seen in the *Tabanidae*. The line of evolution of the forewings of the Myiodaria, then, parallels that of the forewings of the higher Heteroneurous Lepidoptera, in that it consists chiefly of the movement basad, and finally the suppression, of the cubito-median Y-vein, and a great expansion of the more distal portions of the wing. We may profitably contrast the position of the cross-vein *r-m* in the wings of the *Syrphidae* and the *Tachinidae*, and note also the immense increase in the area occupied by the median cell (*mc*) in the latter.

It does not seem necessary here to say much upon the internal Phylogeny of the Diptera. It is quite clear, from the evidence of the wing-venation, that the primary dichotomy must have been into Nemocera and Brachycera, and not into Orthorrhapha and Cyclorrhapha. The Nemocera are properly defined as that line of evolution in which reduction of Rs has been brought about by loss of the fork of R_{4+5} , and in which little or no tendency to a reduction in the distal joints of the antennæ is manifest. The Brachycera, on the other hand, are that line of evolution in which the reduction of Rs has been brought about; reduction is evident in the antennal distalia, leading to the three-jointed type, with arista, as its highest expression. Nature only makes such dichotomies as these *clear-cut*, through the dying-out of intermediate forms. Thus we should neither be surprised nor annoyed, (though it may be very awkward for the framing of good systematic definitions), when we still find, in this Order, a few types which have preserved all four branches of Rs intact (e.g. *Psychoda*, *Pericoma*, *Protoplasa*), or a few more which, while obviously Brachycera as regards the condition of Rs, have still fairly numerous distalia in their antennæ (e.g. *Rhyphus*, *Xylophagus*, *Arthroceras*). The Phylogenist will welcome the presence of these forms, just as heartily as some Systematists will anathematise them; and it should be remembered that the attitude of mind, that puts systematic convenience before natural

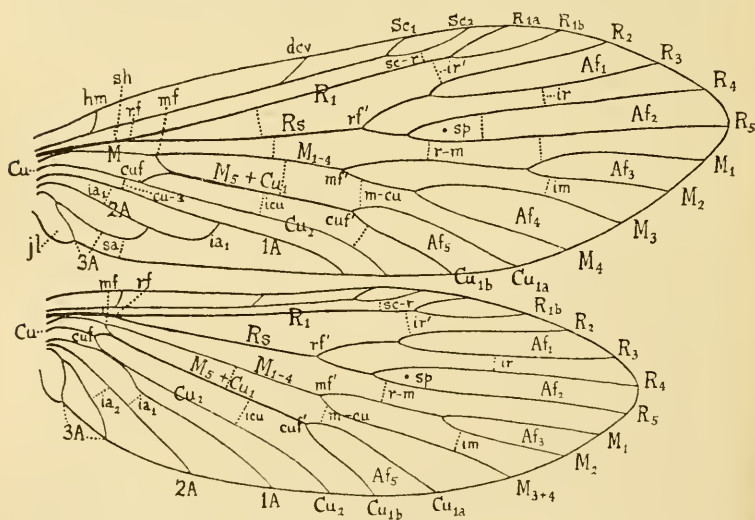
fact, is only slightly removed from that of the famous systematist, who is said to have simplified his task by throwing the "varieties" out of the window. .

Section xiii. THE VENATION OF THE TRICHOPTERA.

(Text-figs. 42, 47b, 71-74.)

Text-fig. 71 shows the venation of the Archetype of this Order. The principal characters to be noted are as follows:—

(1) The pupal wings are merotracheate, the tracheal supply being generally reduced to two tracheæ, which bear no relationship to the imaginal venation. In this character, the Trichoptera



Text-Fig. 71.

Wings of the Archetype of the Order Trichoptera. Lettering as on p. 535.

stand as the most highly specialised of all the Panorpoïd Orders.

(2) Sc and R₁ are distally forked.

(3) The branches of Rs are reduced to four in number; and the apical forks so formed are destitute of cross-veins, except only that between R₄ and R₅, which possesses a cross-vein in the forewing only, as in the Rhyacophilid genus *Psilochorema*.

(4) The dichotomic manner of branching of these forks is retained, with R_{4+5} forking closer to the base than does R_{2+3} .

(5) Between R_4 and R_5 , not far distad from their point of origin, there is a conspicuous *wing-spot*, probably indicating the presence of a special gland or sense-organ. This is a unique specialisation, and is to be found in all Trichoptera except only the highly specialised and reduced *Hydroptilidae*.

(6) The cubito-median Y-vein is completely formed, exactly on the same lines as in *Belmontia*. (See Section iii.)

(7) Fore and hind wings differ in the manner of branching of M_{1-4} . In the forewing, this vein has four branches, forking dichotomously. In the hind, M_{3+4} is always an unbranched vein; so that the total number of branches is reduced to three. (Contrast this with the condition seen in Lepidoptera, in which M_4 fuses distally with Cu_{1a} in both wings).

(8) The cubitus is three-branched, Cu_1 forking distally as in the Paramecoptera, Megaloptera, and Lepidoptera.

(9) In the hindwing, $1A$ fuses with Cu_2 not far from its origin for a short distance, and then diverges from it again.

(10) In the forewing, the three anal veins are looped up to form a double Y-vein. This specialisation is absent from the hindwing.

(11) The costal veinlets are reduced to two, viz. the humeral (*hm*) and the distal (*dco*). (In the peculiar genus *Perisoneura*, of the family *Odontoceridae*, the costal space of the forewing is widened, and carries a set of from six to eight veinlets. As none of the close allies of this genus show any signs of this peculiarity, I am compelled to regard these veinlets as a special development, like the so-called "false cross-veinlets" or "pseudoneuria" of the *Lasiocampidae* in the Order Lepidoptera. In neither case am I able to accept these structures as being truly archaie, and therefore archetypic, characters.)

(12) The cross-vein system is considerably reduced, the following only being present:—the subhumeral (*sh*); the subcosto-radial (*sc-r*); two inter-radials (*ir*, *ir'*), of which one (*ir*) closes the radial cell (*rc*) distally; the radio-median (*r-m*); the inter-median (*im*), closing the median cell (*mc*) distally; the medio-cubital (*m-cu*); the inter-cubital (*icu*); the first inter-anal (*ia_1*); in the forewing only, the cubito-anal (*cu-a*) and the subanal (*sa*); and, in the hindwing only, the second inter-anal

(*ia*₂). Besides these named cross-veins, six extra unnamed ones are shown in the forewing only in Text-fig. 71. These are to be found in the New Zealand genus *Psilochorema* (family *Rhyacophilidae*). The venation of that genus is so peculiar that it may well be that some at least of these cross-veins have been called into being as specialisations to help in adjusting the altered stresses on the main veins; but others may be true ancestral characters, as may readily be gathered by comparing their positions with the cross-veins in *Belmontia* (Text-fig. 63). It has been thought best to include them all in the Archetype, without insisting strongly upon their importance.

In the construction of the Archetype of this Order, one naturally turns first of all to the Liassic *Necrotauliidae*, and to the closely similar *Rhyacophilidae* (Text-fig. 47, *b*), since this family is regarded by all Trichopterists, without exception, as the oldest existing at the present-day. These latter insects have preserved, more than any other family, the original similarity in shape between fore and hind wings, and this shape can be seen to be easily derivable from the more elongated but otherwise similar shape of the Paramecopterous wing, by a slight reduction in the length compared with the breadth of the wing. As I have already pointed out (29), the reduction of the number of branches of *R*s and *M*₁₋₄ to the archetypic condition, and the elimination of any cross-veins originally present in the apical forks, must have been correlated with this shortening.

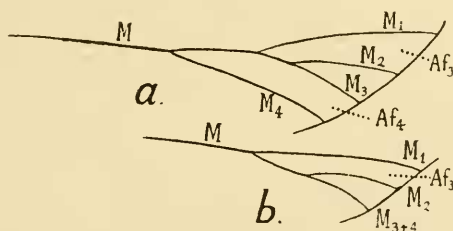
The genus *Rhyacophila* only differs from the Archetype itself in the loss of the cross-veins *ir* and *im*, and in the specialised position of the cross-veins *m-cu* and *cu-a*. Other genera of the family *Rhyacophilidae*, e.g. *Hydrobiosis*, show *ir* in position, but not *im*. This latter cross-vein is, however, very constant in most families, as well as *ir*, and there can be no doubt that the original condition was that in which both the radial and median cells were closed distally by a cross-vein. The families *Polycentropidae* and *Hydropsychidae* show this condition well; the forewings of these families might well be considered even more archaic than that of the *Rhyacophilidae* in consequence, but the hindwing has become broadened out and of very different shape from the fore, and so must be regarded as more specialised. But of how little real significance such changes are, may be gathered from a reference to the Lepidopterous family *Hepialidae* (Section xiv.), where the similarity in shape of the fore and hind

wings is retained in some genera (e.g. *Leto*, Text-fig. 81) and quite lost in others (e.g. *Trictena*, Text-fig. 82).

In constructing the Archetype of this Order, the only difficult points to be decided are (a) the archetypic condition of the media in the hindwing, and (b) the question of including certain cross-veins.

With respect to the media, we have to show, firstly, that a separate M_4 is never present in this wing, and, secondly, that the cross-vein marked *m-cu* is *really* that cross-vein, and not the reduced basal piece of M_4 after fusion with Cu_{1a} as in the Lepidoptera.

A survey of all the known genera of the Order shows that a separate vein M_4 is absent in the hindwings of all except the two rather highly specialised genera *Helicopsyche* and *Saetotricha* (Text-fig. 72), belonging to the family *Sericostomatidae*. In the hindwings of these two genera, Ulmer (33) has considered the three veins present as M_{1+2} , M_3 and M_4 respectively, on the ground that the apical fork lies between the last two of them;



Text-Fig. 72.

Condition of the branches of the media in *a*, forewing and *b*, hindwing of *Saetotricha ptychopteryx* Br. (fam. *Sericostomatidae*), to show transference of M_2 across to M_3 . Lettering as on p. 535.

whereas, in the hindwings of other Trichoptera, it lies between the first two. The mistake in this is easily seen by comparing the fore and hind wings together, when it will be clear (Text-fig. 72) that, in the forewing, M_2 has migrated across from its original position, as the lower branch of M_{1+2} to M_3 , and has thus carried the apical fork along with it. The same specialisation has evidently happened in the case of the hindwing; but, since there is no separate M_4 , the true homologies of the three veins became obscured thereby. In Ulmer's notation, the apical

fork between M_1 and M_2 is called Af_3 , that between M_3 and M_4 , Af_2 . The correct position of these forks is marked in Text-fig. 72 for the genus *Saetotricha*; the condition in most species of *Helicopsyche* is closely similar. It will be noted that there is no true Af_4 in the hindwing, and the correct naming of the lower branch of M is M_{3+4} . Further evidence in favour of this is afforded by the fact that some species of *Helicopsyche* show M_2 arising almost coincidently with M_1 and M_3 (i.e. the migration across from M_1 to M_3 is only half accomplished), and that the genera of *Sericostomatidae* most closely allied to the two under discussion (e.g. *Thremma*), have the three branches of M in the hindwing normally placed.

As regards the nature of the vein which I have marked *m-cu*, we should note the following points:—

(1) In the genus *Rhyacophila*, it descends from *mf'* obliquely to Cu_1 , in the opposite direction to that which it would take if it were portion of a main vein.

(2) In the same genus, an exactly similar vein is present in the forewing also. But, as this wing also has M_4 complete, there can therefore be no doubt whatever that this vein, and its homologue in the hindwing, are both correctly named as the cross-vein *m-cu*.

(3) It is frequently very variable in position, and frequently also quite absent.

(4) It never carries macrotrichia, which it would almost certainly do if it were the basal unfused portion of a main vein.

All the evidence, then, points to this vein being *m-cu*, and hence to there never having been any fusion between M_4 and Cu_{1a} in the Trichoptera comparable with the specialisation seen in both wings of the Lepidoptera. I therefore have no hesitation in naming the lowest branch of M in the hindwings of the Trichoptera M_{3+4} , as shown in the Archetype (Text-fig. 71) and Text-figs. 72, 73.

With respect to the inclusion of certain cross-veins in the Archetype, we may note the following points:—

(1) As the genus *Psilochorema* is exceedingly archaic, I have decided to include the six cross-veins found in the forewing of that genus, over and above the usual ones seen in archaic Trichoptera. One of them, viz. that passing from Rs to M_{1+4} , occurs in almost the same position in *Hydrobiosis*, so that there can be little doubt that it is truly an archetypic character. The

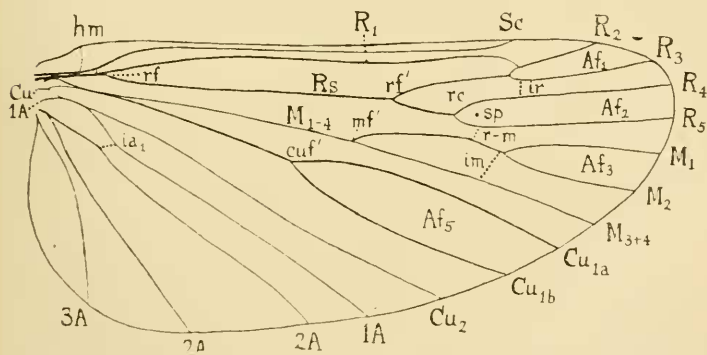
other five are more doubtful, and are only provisionally included until more is known about the venation of these very ancient Rhyacophilids.

(2) The cross-vein *sa* occurs, so far as I am aware, only in the genus *Philopotamus*. But, as a cross-vein occurs in a closely similar position in the archaic Lepidopterous genus *Eriocrania*, I have decided to include it, under the name of *subanal cross-vein*, in the Archetypes of both Orders.

(3) In spite of the formation of the anal Y-vein between 1A and 2A in the forewing, the first inter-anal (*ia*₁) may still be seen clearly present in a number of genera, as also in *Sabatinea* and *Trietena* amongst the Homoneurous Lepidoptera. There is therefore no doubt that this cross-vein is an archetypic character.

Having, then, determined the Archetype of the Order, we may now briefly indicate the main lines of specialisation in the wing-venation within the Order itself. These may be stated as follows:—

(1) *Broadening of the anal area of the hindwing.* In the most archaic family, the *Rhyacophilidae*, fore and hindwings are closely similar in shape, and the anal area of the hindwing only differs from that of the fore in having 1A fused near its base with Cu₂, and the courses of the three anal veins running separate and free to the wing-border, with the two inter-anal



Text-Fig. 73.

Hindwing of an undescribed species belonging to the family *Polycentropidae*, allied to *Stenopsychodes* Ulm., showing the enlarged anal area. Lettering as on p. 535. (x 8).

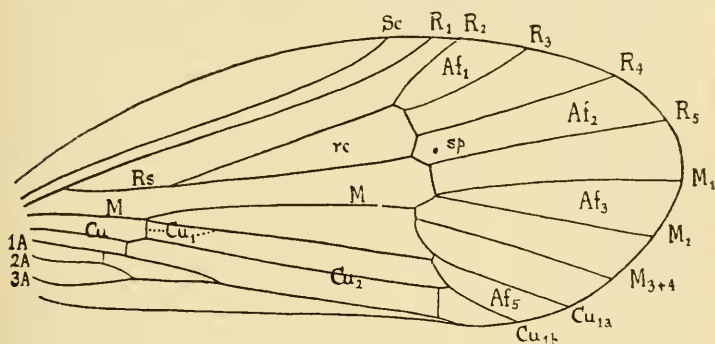
cross-veins (ia_1 , ia_2) placed somewhat longitudinally in position of ia_2 , may still be found in a very archaic genus of *Polycen-tropidae* (a family closely allied to the *Rhyacophilidae*), which has not yet been named, but which is closely allied to *Stenopsychodes* Ulmer, as shown in Text-fig. 73. It will be noticed that 2A appears to have forked; and, of course, both 2A and 3A have become greatly lengthened. This hindwing is figured partly for the purpose of drawing attention to the fact that the inception of heteroneurism may be taken as undoubtedly due to the widening of the anal area of the hindwing, together with the narrowing of its costal and subcostal areas. Both these conditions are well shown in Text-fig 73. If the line of specialisation had been continued, in this case, by further narrowing of the anterior portion of the wing, affecting the radial area, and bringing about (a) a fusion of Sc and R_1 , as occurs in many Trichoptera, and (b) a reduction of Rs to a simple, unbranched vein, there would have resulted a group of heteroneurous Trichoptera exactly parallel with the Suborder Heteroneura within the Lepidoptera.

The amplification of the hindwing may be seen in other families of the Trichoptera, especially in the *Hydropsychidae* and the *Limnephilidae*, and is very greatly accentuated in some genera of these two families.

(2) *Narrowing of both wings, with loss of certain main veins.* This is carried to an extreme in certain *Leptoceridae*, *Molanidae* and *Hydroptilidae*. All stages of the reduction-process may be studied in the various genera of any one of these families; but there does not seem to be any definite plan by which the main veins are reduced. Moreover, owing to the lack of the precedent tracheation in the pupal wings, it is a very difficult matter to decide, in many cases, what are the correct names of the veins left over.

(3) *Alignment of the distal cross-veins to form a single transverse series.* This line of evolution is followed out in the forewings of the dominant family *Limnephilidae*, which is really the only family of Trichoptera which may be said to have evolved a venational scheme of its own. The first stage in this line of evolution is the formation of the two separate *anastomoses*, viz. the *upper anastomosis*, formed by the alignment of the basal piece of R_3 the cross-vein ir , the basal pieces of R_4 and R_5 ,

and the cross-vein *im*, as an irregular, transverse zig-zag from the base of the second apical fork to the base of M_{1+2} ; and the lower anastomosis, formed by the basal piece of M_{3+4} , the cross-vein *m-cu*, and a highly specialised arrangement of the ends of the branches of Cu and the cross-vein *icu*, as a second irregular, transverse zig-zag line, taking in the base of the fifth apical



Text-Fig. 74.

Forewing of *Chaetopteryx villosa* (Fabr.), after Ulmer, but with lettering added, to show the formation of the anastomosis. Lettering as on p. 535.

fork. The highest stage in this evolution is the alignment of the upper and lower anastomoses to form a single transverse zig-zag line, called simply *the anastomosis*, running from the fork of R_{2+3} right across the wing. This is to be seen in such genera as *Chilostigma* and *Chaetopteryx* (Text-fig. 74).

The formation of the anastomosis in the family *Limnephilidae* recalls the analogous formation called by the same name in the Order Perlaria.

For a comparison of the Archetypes of the Trichoptera and Lepidoptera, see pp. 634-5.

Section xiv. THE VENATION OF THE LEPIDOPTERA.

(Plates xxxii.-xxxv., figs. 17-24 and Text-figs. 36b, 53-56, 58-59, 75-103.)

The venation of the Archetype of this Order is shown in Text-fig. 75, which should be carefully compared with that of the Trichoptera in Text-fig. 71. The following are the chief points to be noted:—

distal Y-vein (Section vi.). This character is best shown in the *Hepialidae*.

(8) The cubitus is three-branched, Cu_1 forking distally as in the Paramecoptera, Megaloptera, and Trichoptera.

(9) In the hindwing, 1A fuses with Cu_2 not far from its origin for a short distance, and then diverges from it again. This character is to be seen in the Jugo-frenata, *Hepialidae* and in quite a number of the older Heteroneura. It also occurs in all Mecoptera and Trichoptera, in the Raphidioidea and some Planipennia.

(10) In the forewing, 2A is looped on to 1A, and 3A on to 2A, thus forming a double Y-vein as in Trichoptera. This character is to be found in *Mnemonica* and *Sabatinca*, the two most archaic genera in the Jugo-frenata, but is usually reduced to a single Y-vein, formed by 1A and 2A only, in the other genera of that group. Throughout the Lepidoptera, 3A tends to become obsolete in the forewing, and is absent from most forms, including the *Hepialidae*.

(11) There is only one costal veinlet, viz. the humeral, *hm*. In many pupal wings, this is seen to be supplied by a special trachea running alongside Sc. (Text-figs. 80, 85). This is certainly the homologue of the formation to be seen in the Paratrachoptera (Text-fig. 65).

(12) The cross-vein system is even more reduced than in the Archetype of the Trichoptera, only the following being present:—the subcosto-radial (*sc-r*); the inter-radial (*ir*) closing the radial cell (*rc*) distally; the radio-median (*r-m*); the inter-median (*im*) closing the median cell (*mc*) distally; the cubito-anal (*cu-a*); the first inter-anal (ia_1); the second inter-anal (ia_2) in the hindwing, and the sub-anal (*sa*) in the forewing only. This last is only to be seen in *Eriocrania* (27, and Text-fig. 53, c).

Thus, quite apart from the six unnamed cross-veins which, since they are present in the Rhyacophilid genus *Psilochorema* have also been included in the venation of the Archetype of the Trichoptera, the following cross-veins present in that Archetype are absent from the Archetype of the Lepidoptera:—the sub-humeral (*sh*); the inter-radial from R_1 to R_2 (ir'); the medio-cubital (*m-cu*),—owing, of course, to the fusion of M_4 with Cu_{1+2} ; and the inter-cubital (*icu*). Thus the cross-vein system of the Lepidoptera is archetypically considerably more reduced than that of the Trichoptera.

The Archetype of the Lepidoptera, as here defined, includes, of course, characters taken from the three archaic Jugo-frenate families of the Homoneura, viz. the *Micropterygidae*, *Eriocraniidae* and *Mnesarchaeidae*. It was realised from the first that the question of the correct ordinal position of these families was of the greatest importance; and this was one of the reasons that prompted me to devote special attention to them, giving a series of papers on them, to be read concurrently with those of which this paper forms a part. As soon as the study of these three families had progressed sufficiently, I became convinced that they were indeed archaic Lepidoptera, and nothing else; and hence I do not now hesitate to use them in constructing the Archetype of that Order. But, in order that those who may still hold an opposite view may be convinced that it makes no essential difference whether they be included or not, from the point of view of the *archetypic wing-venation*, the alterations which would be caused in the definition of the Archetype are here set down, as follows:—

(A) If the family *Micropterygidae* (s.str.) be excluded, then there will be no difference at all in the Archetypic wing-venation. For Sc is distally forked in *Prototheora* and in *Mnemonica*, R_1 is distally forked in both *Mnemonica* and *Eriocrania*, *sc-r* is present in *Mnesarchaea*, the other cross-veins in numerous genera, and likewise the fusion of $1A$ with Cu_2 in the hindwing.

(B) If all the three families of the Jugo-frenata be removed from the Lepidoptera, then the Archetype must be modified, in so far that R_1 will be no longer forked, and the cross-veins *sc-r*, ia_2 , *sa*, will be absent; since, as far as I know, these characters do not occur outside the Jugo-frenata. All the other characters are to be found in one or more of the remaining families of the Order. As the differences mentioned are not of very great importance, it will readily be seen that no *essential* alteration will be needed in the venation of the Archetype, even if the whole of the Jugo-frenata were to be removed from the Order.

The relationship between the two Orders Trichoptera and Lepidoptera is a close one, comparable with that between the Megaloptera and Planipennia, but not so close as this latter. In each case, it is the aquatic side-branch (Trichoptera or Megaloptera) which has remained, on the whole, in the more archaic condition, while the main terrestrial stem (Planipennia or Lepidoptera) has advanced, and branched out in many new direc-

tions, and has become far more abundant in families, genera and species. But it is essential that we should see clearly that neither the Lepidoptera nor the Planipennia are of aquatic origin, and neither can possibly be derived from its closely related aquatic Order. The close similarity between the archetypic venations of the Trichoptera and Lepidoptera will be sufficiently obvious from a perusal of the characters already set down, and the archetypic diagrams (Text-figs. 71, 75). Their differences are perhaps not so obvious; but they are of very great importance for the right understanding of the phylogenetic problem, and are set down in the accompanying Table (Table ii.)

TABLE II.

TABLE OF DIFFERENCES IN THE WING-CHARACTERS OF THE ARCHETYPES OF THE TRICHOPTERA AND LEPIDOPTERA.

| | Character. | TRICHOPTERA | LEPIDOPTERA |
|-----|---|--|--|
| (1) | Pupal Wing | Merotracheate | Holotracheate |
| (2) | Condition of M_4 | Present in forewing as a separate vein; absent from hindwing | Present in both wings, but distally fused with Cu_{1a} . |
| (3) | Wing-spot between R_4 and R_5 | Present | Absent |
| (4) | Cross-veins <i>sh</i> , <i>ir'</i> , <i>m-cu</i> , and <i>icu</i> . | Present | Absent |
| (5) | Functional frenulum | Absent | Present |
| (6) | Macrotrichia specialised as scales | Absent | Present |

With respect to these six differences, the Trichoptera are the more archaic in (4) and (6), and in (2) as regards the forewing only; the Lepidoptera are the more archaic in (1), (3) and (5), and in (2) as regards the hindwing only. Thus the specialisations are fairly equally divided between the two Orders; and it is evident, on more than one count, that neither can be ancestral to the other. They must have arisen as a dichotomy from a common stem, which combined the archaic characters of both Orders.

We must now consider a little more fully the venation of the Lepidoptera, in order to show quite clearly how the archetypic characters have been determined.

It will not be necessary, at this stage, to attempt to prove what is by now universally admitted, viz. that the Suborder Homoneura contains the most archaic existing types of the Order. Also the space at my disposal will not allow of a full review of the characters of the venation, in all families of the huge Suborder Heteroneura. I propose, therefore, to take the families of the Homoneura in order, and study their venation; and then to select only those archaic families of the Heteroneura which will help to elucidate the main problem, together with a few other types which may throw light on important, though subsidiary, problems, such as the origin of the Butterflies. In doing this, it will have to be borne in mind that many of the archetypic characters have already been determined from the evidence in previous Sections, which will be referred to when required.

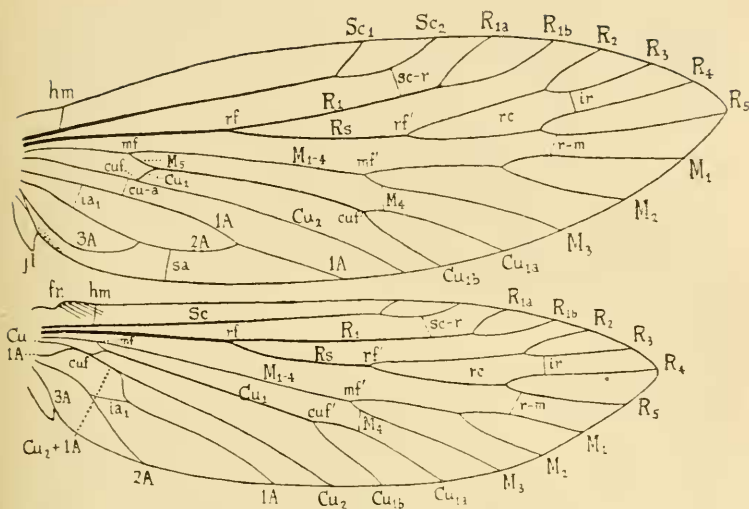
Suborder **Homoneura**.

Division **Jugo-frenata**.

This division contains only the three families *Micropterygidae*, *Eriocraniidae*, and *Mnesarchaeidae*.* As a study of their venation, and its relationships with that of the Trichoptera, would have unduly enlarged this Part, the work has already been done separately (26), and the results are taken for use in this paper. In Text-fig. 76, I have given a diagrammatic representation of the Archetypic venation of the Jugo-frenata, by including in the one figure all the archaic characters to be found in the whole of the genera belonging to this division. The distribution of these characters may be gathered both from my previous paper (26) and, as regards the separate families, from the Table given on p. 650. It is only necessary here to call attention to the characters in which the Jugo-frenata themselves are specialised,—in other words, those characters in which the venation given in Text-fig. 76 differs from that of the Archetype of the Order Lepidoptera. These are:—

(1) The far distal position of the forks rf' and mf' . This is an important specialisation, frequently present in *highly reduced forms*, or as the result of stenogenesis. Its presence in the Jugo-frenata is proof that they are of smaller size than the Archetype of the Lepidoptera, which probably came closer to *Belmontia* in size.

*I propose to treat these as three distinct families from this Part onwards.



Text-Fig. 76.

Wings of the Archetype of the Division Jugo-frenata. Lettering as on p. 535.

(2) The loss of the original obliquity of M_4 after fusion with Cu_{1a} . This, again, is due to reduction in size. In the larger *Hepialidae*, the obliquity is retained; while, in the *Prototheoridae*, the reduction of M_4 to the appearance of a cross-vein has not proceeded so far as in the Jugo-frenata. (Reference should be made here to the Note on the Evidence concerning the Existence of vein M_4 on p. 651.)

(3) The cross-vein *im* is never present. This is an important specialisation, seeing that this cross-vein closes the median cell (*mc*) not only in the rest of the Homoneura, but also in Heteroneura, and plays its part in the formation of the large basal cell. The loss appears to be due directly to the removal of *mf'* distad, and is therefore to be traced back, like the other specialisations, to reduction in size.

It will be seen from the Table given on p. 650 that the *Micropterygidae* are the most archaic family of Lepidoptera still existing, but that they fall far short of possessing the full number of archaic characters exhibited by the Archetype of the Order, as regards the Wing-venation. The *Eriocraniidae* are somewhat

more specialised, being about level with the *Hepialidae* in the percentage of archaic characters which they possess. The *Mnesarchaeidae* are the most highly specialised of all the Homoneura.

The manifest agreements between the venational schemes of the Archetypes of the Jugo-frenata and the Trichoptera are clearly of the utmost importance, since it is on these that Comstock (15) has removed the former to the latter Order. They may be stated as follows:—

- (1) Sc and R₁ are distally forked.
- (2) The branches of Rs are four in number and dichotomously arranged.
- (3) The radial cell is closed distally by *ir*.
- (4) The cubito-median Y-vein is completely formed.
- (5) The cubitus is three-branched, Cu₁ being forked distally.
- (6) The anal veins of the forewing form a double loop or Y-vein.
- (7) In the hindwing, 1A fuses with Cu₂ for a short distance not far from the base, and then diverges from it and runs separately to the wing-border.

(8) The cross-vein system in the Jugo-frenata is closely similar to that of most archaic Trichoptera, although *im* is always absent. In particular, *ia*₁ in the hindwing is longitudinally placed.

With one exception, all the above characters are to be found, not only in Trichoptera and Jugo-frenata, but also in either (a) other Panorpooid Orders, or (b) other Lepidoptera. The exception is (6). The double Y-vein formed by the looping up of the three anal veins is peculiar to the Trichoptera and to the genera *Mnemonica* and *Sabatinea* amongst the Jugo-frenata. In the other genera, it is either absent (replaced by the single Y-vein usual in Lepidoptera) or occasionally more or less clearly formed. If the complete double-Y formation is the more archaic condition, then it is clear that it must have been inherited from the common ancestor of both Trichoptera and Lepidoptera; but, while the Trichoptera have retained, and, in many cases, elaborated it, the Lepidoptera, on the other hand, almost immediately began to lose it, through degradation of the vein 3A. If, however, the single Y-vein be the older formation, then the already present tendency towards further specialisation must have produced the double-Y formation independently in the Trichoptera and in those Jugo-frenata which possess it, while most of

the Lepidoptera failed to reach this stage, through degradation of 3A. In either case, the condition of these veins in the Jugo-frenata is no argument for placing that group in the Trichoptera, as Comstock has done (15); since the group, as a whole, shows the Trichopterous condition in certain genera and the Lepidopterous condition in others (see 27, Text-figs. 1, 6, 9, showing the single loop present in *Eriocrania*, *Micropteryx* and *Mnesarchaea*).

As regards character (8) above, it should be noted that the longitudinal position of the cross-vein *ia*¹ in the hindwing, which Comstock imagined was peculiar to the Trichoptera and the Jugo-frenata, is also to be found in the Mecoptera and the *Sialidae* (Text-fig. 104). This cross-vein does not occur, so far as I know, in the hindwings of any Lepidoptera outside the Jugo-frenata.*

We may say, then, of the eight characters named above, which are common to the Trichoptera and Jugo-frenata, that they are all of them, except (6), also to be found outside these two groups. Taken together, they form a strong argument for the close relationship of the two Orders Trichoptera and Lepidoptera. But they do not, in any sense whatever, justify the removal of the Jugo-frenata to the Trichoptera.

The complete venational characters of the Jugo-frenata may be gathered from my paper on this group (26). We shall now proceed to discuss the venations of the other two families of the Homoneura, and to note in particular the many points of resemblance between them and the Jugo-frenata.

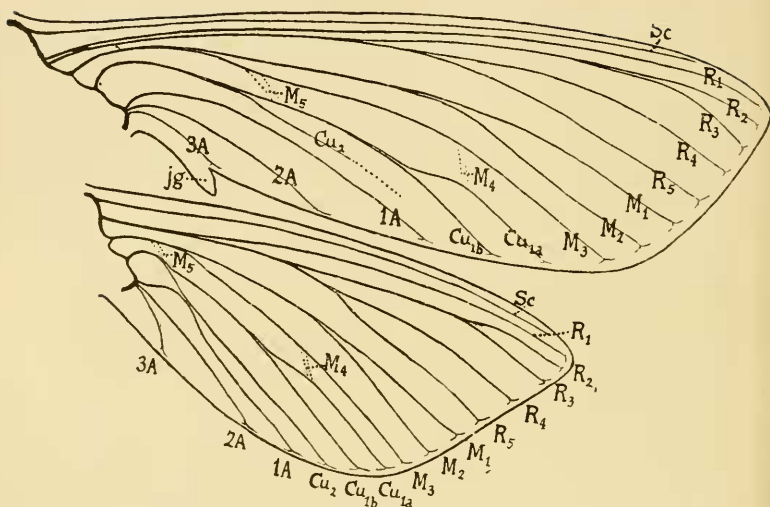
Division Jugata.

Family HEPIALIDÆ.

This family is of the greatest importance for the correct understanding of the Archetype of the Lepidoptera.

Most of the pupæ studied belonged to species of the genus *Charagia*, the larvæ of which tunnel in the stems of various trees. Text-fig. 77 shows the tracheation of the wings in a freshly-turned pupa of *Ch. splendens* Scott. This pupa was first examined under a lens, while it rested on cotton-wool. The

*The complicated condition of the anal venation at the base of the hindwings of certain *Tortricina* suggests that this cross-vein may sometimes be present there. See, for instance, the figure given for *Isotrias* by Meyrick (3, p.542).



Text-Fig. 77.

Tracheation of wings of freshly formed pupa of *Charagia splendens* Scott. (x 3·4). Lettering as on p. 535.

tracheation of the forewing, and that of the hindwing underlying it obliquely, could be clearly seen; and drawings were made of them. As soon as the pupa had hardened up a little, it was killed with chloroform, and the outer covering of the forewing was dissected off. This exposed the tracheæ of the forewing *in situ*, including their basal connections. A drawing was made of these, under the camera lucida; and then the whole wing was carefully dissected off and floated out on to a slide, where the bases of the tracheæ were photographed (Plate xxxii., fig. 17). Next, a camera-lucida drawing of the hindwing tracheæ was made, the fine membrane separating this wing from the fore having been dissected away. Text-fig. 77 combines the two camera-lucida drawings of the wings *in situ*, and therefore represents the wing-tracheation of a pupa less than twelve hours old.

At this early stage, the courses of the future veins are not clearly indicated; but I have marked the positions of the two exceedingly delicate bands which very soon appear, indicating the positions of M_5 and M_4 , forming the upper arms of the

cubito-median and distal Y-veins respectively. Neither of these veins is preceded by a trachea in the freshly-turned pupa. Other points to be noted are:—

(1) The composite origin of R, which is particularly noticeable in the forewing.

(2) The composite origin of M (See Plate xxxii., fig. 17).

(3) The fact that Cu² is already reduced in the forewing.

(4) The very distinct origin of the anal group of tracheæ, in a single bunch far removed from Cu, with all three anal tracheæ clearly indicated.

(5) The fusion of 1A with Cu² in the hindwing, for a short distance near the base. This latter character is claimed by Comstock to be peculiar to the Trichoptera; but, as it also occurs in the *Jugo-frenata*, it is used as part of the argument for removing those insects to the Trichoptera (15).

(6) The complete separation of the three anal veins in the forewing, except at their bases.

Pupæ dissected at ages from a few days to more than a week old show little difference from the above. The wing becomes generally more opaque, leaving the paler and more transparent bands, along which the imaginal venation is later laid down, clearly visible. No trachea was seen by me along the course of M₅ in any pupa of this age, nor did I ever succeed in finding a trachea along the course of M₄ in any pupa of any age whatever.

In the older pupæ, the wing becomes darkened; and, with a little care, it may be removed whole from its sheath, without damage. The base becomes narrowed, so that the condition of the basal tracheation is completely altered. The formation of scales becomes very apparent, and greatly hinders the study of the tracheæ *in situ*. In order to make out the courses of the tracheæ near the base, I cleared some of the wings very rapidly in chloro-phenol*. There is usually only just time to see the condition of the tracheæ plainly, when this strong clearing agent is used; for the tracheæ are no sooner cleared than they begin to shrivel up, so that drawings must be made at once.

In a pupa which was evidently only a few days from metamorphosis, seeing that the colouration of the wings was beginning

*I have to thank Dr. H. Priestley, Lecturer in Physiology, University of Sydney, for bringing this strong clearing agent to my notice.

to be evident, a fairly strong trachea was seen traversing M_5 , in the forewing; but this trachea was not of so large a calibre as the cubital trachea, which still ran strongly in the lower arm of the Y-vein. There is no trachea in M_4 . Trachea Cu_2 is still further reduced in the forewing. The anal area has become very much narrowed, and tracheæ 2A and 3A are very much reduced in the forewing. In the hindwing, the fusion of Cu_2 with 1A remains, but has approached nearer to the base of the wing, as has also the position of M_5 in both wings. This points to a great contraction of the base of the wing in the late pupa, and this contraction is very much further emphasised at metamorphosis, when the more distal part of the wing becomes much expanded.

It is necessary here to point out that trachea M_5 does not always appear in the late pupa. In some cases, it may be seen as a very small trachea indeed; while, in one pupa of *Leto*, examined only a few days before metamorphosis, there was still no sign of it.

If a freshly-emerged Hepialid imago be taken and killed, and its wings carefully descaled and cleared, the tracheæ may be found *in situ*, running in the veins, very much as they are to be seen in the late pupa. The principal changes that take place at metamorphosis are as follows:—

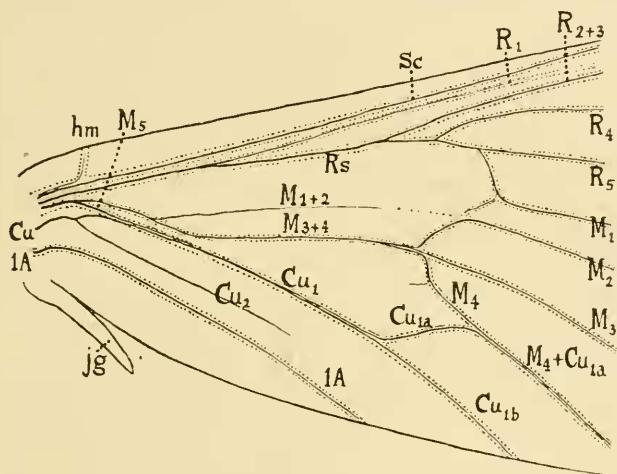
(1) The base of the wing, already reduced in size in late pupal life, undergoes practically no expansion. On the other hand, the more distal portion expands greatly, so that the final result is to bring the primary median and cubital forks very much closer to the base of the wing than they were in the pupa.

(2) Trachea M_5 is frequently of large calibre, and may be considerably larger than trachea Cu_1 . There is, however, a great deal of variability in this character, as I have examined a number of imagines in which trachea Cu_1 was considerably the stronger of the two.

(3) Trachea M_4 is usually absent; but it was present in a fair number of wings, and in some cases it was even of larger calibre than trachea Cu_{1a} . In a few specimens, I have seen the latter quite aborted; but in most cases, when present, the two tracheæ run side by side along the stem of the distal Y-vein, $M_4 + Cu_{1a}$. (For details, see Section vi.)

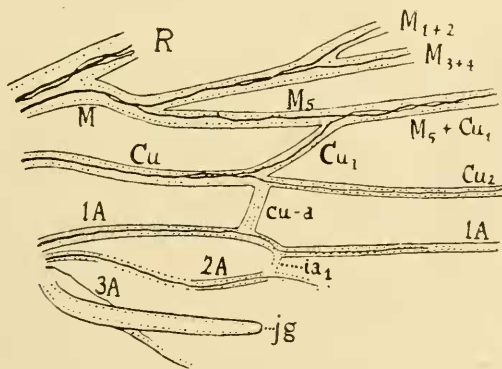
(4) In the case of *Ch. splendens* (Text-fig. 78) scarcely any trace of either 2A or 3A is left in the forewing of the imago,

and there is not at any time any formation of an anal loop or Y-vein between 1A and 2A. The most complete condition of the



Text-Fig. 78.

Basal part of forewing of *Charagia splendens* Scott, to show the venation (double dotted lines) and the tracheation. (x 4). Lettering as on p.535.



Text-Fig. 79.

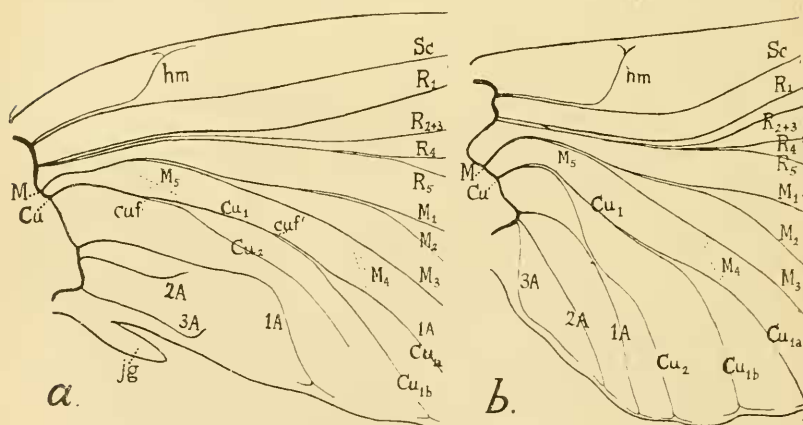
Basal part of forewing of *Trictena labyrinthica* Don., to show the incomplete formation of the anal Y-vein, and the presence of the cross-vein *ia*₁. (x 4½). Lettering as on p.535.

anal veins is to be seen in the forewing of *Trictena labyrinthica* (Text-fig. 79), in which this loop is completed by the intervention of the interanal cross-vein ia_1 .

The conclusions to be drawn from the above are, I think, that, on the whole, the freshly-turned pupa gives us the most primitive condition of the wing-tracheation; that the tracheation of the imaginal wing shows a considerable amount of specialisation; and that the development of tracheæ M_5 and M_4 , the former late in pupal life, the latter occasionally at metamorphosis, may well represent the late appearance of tracheæ which are in process of being lost altogether.

We may now turn our attention to the genus *Leto*, of which I was able to dissect several pupæ obtained for me by Mr. Luke Gallard. These pupæ are of very large size, some being four inches long, so that their dissection is a fairly easy matter, and the tracheation can be studied under a low power.

Text-fig. 80 shows the bases of the wings in an early pupa of *Leto staceyi* Scott, dissected off and floated out upon a glass slide in water. If these be compared with *Charagia* (Text-fig. 77) it will be seen that there are some important differences, as follows:—



Text-Fig. 80.

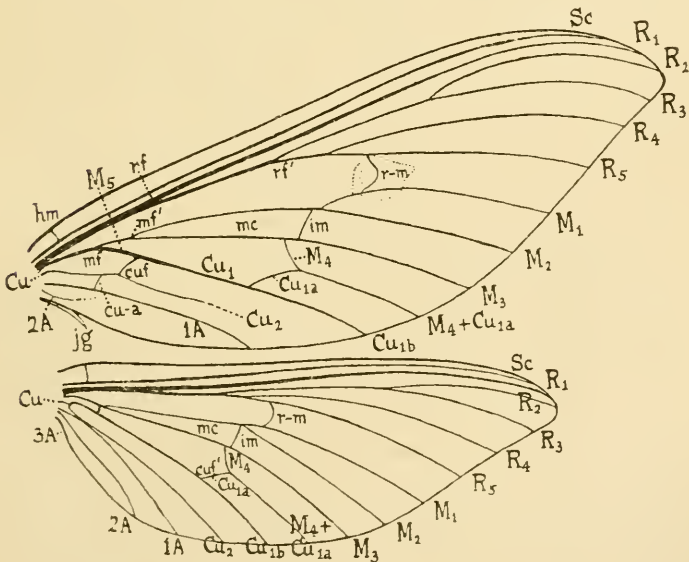
Basal portion of tracheation of *a*, forewing, *b*, hindwing, in the freshly formed pupa of *Leto staceyi* Scott. (x 3). Lettering as on p. 535.

(1) The humeral veinlet, *hm*, is supplied by a special trachea which rises with Sc and runs alongside it for some distance. This might be the remnant of the old costal trachea, but is more likely to be a true basal branch of Sc. In any case, it should be noted that the condition seen here in the pupal wing is closely paralleled in the fossil genus *Aristopsyche* of the Order Paratrichoptera (Text-fig. 65). It is also to be found in the pupæ of the *Cossidae* (Text-figs. 85, 86).

(2) In the forewing, trachea 2A is short and tends to bend up towards 1A, thus indicating a tendency towards the formation of the single anal Y-vein found in most Lepidoptera.

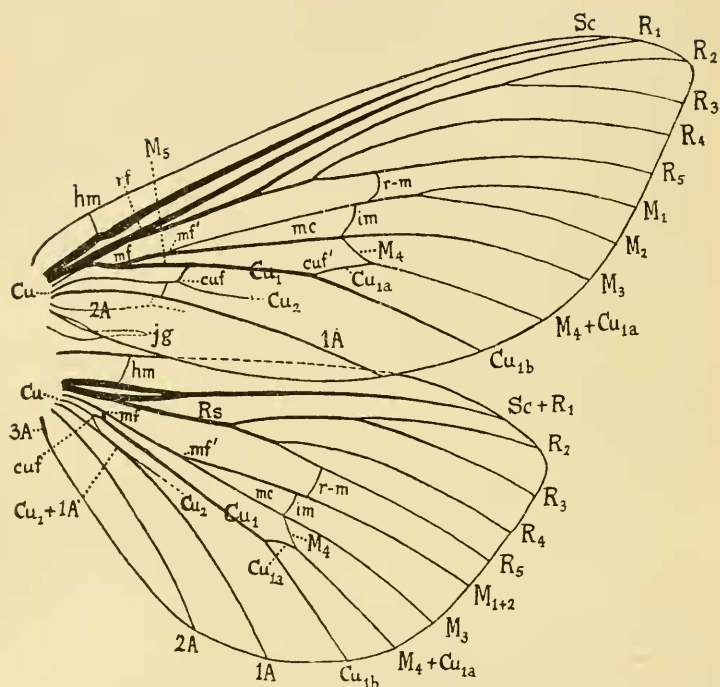
(3) In the forewing the anal group of tracheæ arises differently from that of *Charagia*, the individual members being more widely separated. They are all, however, far removed from Cu, which is close up to M. In the hindwing, the anal group is much the same as in *Charagia*.

As before, I have marked by double dotted lines the positions



Text-Fig.81.

Leto staceyi Scott, imaginal venation (x 0.8). Lettering as on p.535.



Text-Fig. 82.

Trictena labyrinthica Don., imaginal venation. ($\times 1\frac{1}{2}$). Note the loss of the fork of M_{1+2} in hindwing. Lettering as on p. 535.

of the veins M_5 and M_4 , which very soon begin to appear as pale bands with the rest of the imaginal venation. A very important character, viz. the partial fusion of $1A$ with Cu_2 in the hindwing, is as clearly shown in this genus as in *Charagia*. But, in the first pupa which I dissected, and which I figured in a previous paper (27, Text-fig. 14), this fusion was not present. An examination of the photomicrographs which I took of this pupal wing shows me quite clearly that this was due to displacement while lifting the wing and spreading it out on the slide; for the pale bands which indicate the imaginal venation can be seen fused together between the two tracheæ, which are clearly pulled slightly out of their correct positions. Three other pupæ since dissected all agree in having this fusion clearly marked.

The genus *Leto* differs from all other Australian genera in the possession of a large raised eye-spot on the forewing, covering the cross-vein *r-m*, which forms the top of the ridge, and also in the very close similarity in shape between fore and hindwings, as can be seen from Text-fig. 81.

As a contrast to *Leto*, I show in Text-fig. 82, the venation of the genus *Trictena*, of which, unfortunately, I have not been able to obtain pupæ, but only freshly emerged imagines. Here the difference in shape between fore and hindwing is very great, and is typically that of a Heteroneurous rather than a Homoneurous type. Moreover, the tendency towards heteroneurism is very evident from the fact that there is a vein missing in the hindwing, M_{1+2} being a simple vein, and also because, as in the hindwings of Heteroneura, *Sc* and R_1 have coalesced near their bases, and run together as a single fused vein to the wing margin. The genus, then, is a living illustration of the manner in which a heteroneurous type can be evolved from a homoneurous type. It does not, however, indicate the actual line of evolution of the Suborder Homoneura; because, in their case, it is not the branches of *M* which become suppressed in the hindwing, but the branches of *Rs*. Reduction of the branches of *M* along the lines indicated in this genus might well have led to the Jurassic fossil family *Palaeontinidae* (p. 654), which, if Handlirsch's restorations be correct, were strongly heteroneurous, but had *M* reduced to a simple vein in the hindwing.

Family PROTOTHEORIDÆ.

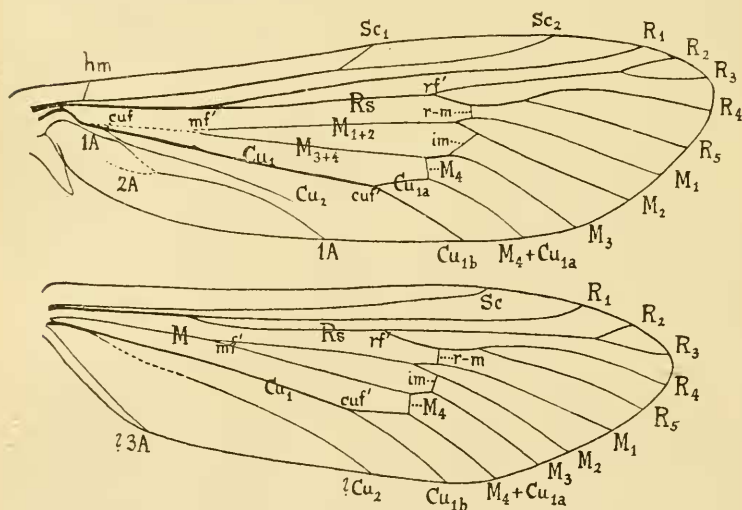
This family was founded by Meyrick (9) to contain a remarkable moth from South Africa, *Prototheora petrosema* Meyr., which is in some respects intermediate between the *Jugo-frenata* and the *Hepialidae*. For material of these rare insects I have to thank Dr. L. Peringuey, Director of the South African Museum, Capetown.

The material sent by Dr. Peringuey, when examined, was found to contain two very distinct species, one of which was probably the same as Meyrick's type, the other very distinct from it. No figures of the venation of these interesting insects have yet been published. Text-fig. 83 shows the venation of the more bluntly winged species (the other has the wings more pointed at apex, with unimportant differences in the venation).

The family agrees with the *Hepialidae* in possessing a true

jugum, and in lacking all traces of a frenulum; therefore it is rightly included in the division Jugata. It also agrees with the *Hepialidae* in the basal positions of *rf* and *mf'* (though *rf'* is removed far distad), in the absence of the cross-vein *ir*, in the presence of *r-m* and *im*, and in still showing some indication of the original oblique position of the unfused basal portion of *M*₄. In having a definite branch of *Sc* (*Sc*₁) in the forewing, it is more archaic than most *Hepialidae*; but this condition is closely similar to that seen in *Sthenopis*.

The most remarkable specialisation to be seen in the *Prototheoridae* is the reduction of the venation of the anal area. In the forewing, 1A curves up so as just to touch *Cu*₂, thus recalling the fusion of these two veins in the hindwings of the



Text-Fig. 83.

Prototheora sp. (Table Mountain, South Africa), imaginal venation. (x 6). Lettering as on p. 535.

Hepialidae and *Jugo-frenata*. 2A is obsolescent, being represented only by its distal end joined on to 1A; this character proves that the anal Y-vein formed from 1A and 2A was complete in this wing, before the obsolescence of 2A began. There is a small, weak 3A bordering the jugum distally, in the usual

position. In the hindwing, the whole anal area is devoid of veins, except for one very close to the wing-border, the homologies of which cannot be determined with certainty, and a vein running below Cu_1 , in the usual position of Cu_2 , which may be either that vein or 1A.

In the forewing, M is very completely fused basally with Cu, so that all traces of the cubito-median Y-vein are lost. The main stem of M_{1-4} is obsolescent as far as mf' . In the hindwing, this main stem is more clearly shown, and is not fused with Cu; a tiny remnant of the cubito-median Y-vein appears to be visible at the extreme base of the wing.

The discovery of this family is chiefly interesting in that it proves the existence of hitherto unsuspected Homoneurous types. It may reasonably be hoped that further discoveries along similar lines may yet be made. Indeed, the discovery of the remarkable genus *Anomoses* in South Queensland by Dr. A. J. Turner (31) is probably a case in point; for this genus does not appear to be a true Jugo-frenate type, and should probably be placed either in the *Prototheoridæ* or in a new family *Anomosetidæ*.

In concluding this account of the Suborder Homoneura, it is interesting to compare the wing-venational characters of the five families represented therein, in such a way that the archaic characters in each family may be readily picked out. This is best done by means of a Table (Table iii.), in which the most archaic condition of each separate character is represented under the letter A, while B, C, . . . represent more specialised conditions of the same, in ascending order. The Archetype of the Homoneura will possess all the archaic conditions indicated under A. The "percentage archaism" of that Archetype will therefore be 100. For comparison with this, the "percentage archaism" of each of the five families is worked out in the last column of the Table. When we have studied the Heteroneura, and tabulated their characters in the same manner, it will be seen that that Suborder does not possess a single archaic condition which is not also to be found somewhere within the Suborder Homoneura. In other words, the Archetype of the Homoneura is also the Archetype of the Order Lepidoptera as a whole.

TABLE III.

TABLE OF THE PRINCIPAL VENATIONAL CHARACTERS FOR THE FAMILIES OF THE HOMONEURA.

| Ref. No. | Character. | Jugo-frenata | | | Jugata | |
|---|--|-------------------------------|----------------------------|------------------------------|--------------------|-----------------------------|
| | | <i>Micropter- ygidae.</i> | <i>Eriocran- inae.</i> | <i>Mnesarchae- inae.</i> | <i>Hepialidae.</i> | <i>Proloth- oridae.</i> |
| (1) | Forking of Sc.—A. Present in both wings. B. Present in forewing only. C. Absent in both wings. | A or B. | B or C. | C. | B or C. | B. |
| (2) | Forking of R ₁ :—A. Present in both wings. B. Present in forewing only. C. Absent in both wings. | B or C. | A or B. | C. | C. | C. |
| (3) | Number of branches of Rs:—A. Four in both wings. B. Four in forewing, three in hind. C. Three in both wings. | A. | B or C. | C. | A. | A. |
| (4) | Manner of branching of Rs:—A. Dichotomic. B. Otherwise. | A. | B. | B. | A. | A. |
| (5) | Closing of radial cell distally by <i>ir</i> :—A. Present. B. Absent. | A. | B. | B. | B. | B. |
| (6) | Positions of <i>rf'</i> and <i>mf'</i> :—A. Both normal. B. <i>mf'</i> normal, <i>rf'</i> removed distad. C. Both removed distad. | C. | C. | C. | A. | B. |
| (7) | Number of branches of M ₁₋₄ :—A. Four; M ₄ oblique and fused distally with Cu _{1a} . B. Apparently only three, M ₄ being reduced to a short transverse vein. | B. | B. | B. | A. | B. |
| (8) | Cubito-median Y-vein:—A. Well developed. B. Reduced or absent. | A. | A. | B. | A. | B. |
| (9) | Closing of median cell distally by <i>im</i> :—A. Present. B. Absent. | B. | B. | B. | A. | A. |
| (10) | Number of branches of Cu:—A. Three, all complete. B. Three, but Cu ₂ reduced in one or both wings. | A. | A. | B. | B. | B. |
| (11) | Cubito-anal Y-vein in hindwing:—A. Complete. B. Absent. | A. | A. | B. | A. | B. |
| (12) | Anal veins:—A. All three present. B. 3A absent. C. Only one complete anal present. | A. | A. | A or B. | B. | C. |
| (13) | Anal Y-vein of forewing:—A. Double Y complete. B. Single Y complete. C. Single Y reduced. | A or B. | A or B. | C. | C. | C. |
| (14) | Humeral veinlet <i>hm</i> :—A. Present in both wings. B. Present in forewing only. C. Absent in both wings. | B or C. | A or B. | C. | A. | B. |
| (15) | Cross-vein <i>sc-r</i> :—A. Present in both wings. B. Present in one wing only. C. Absent. | A or B. | C. | B. | C. | C. |
| (16) | Cross-vein <i>r-m</i> :—A. Present in both wings. | A. | A. | A. | A. | A. |
| (17) | Cross-vein <i>cu-a</i> in forewing:—A. Present. B. Absent. | A or B. | A. | A. | A. | B. |
| (18) | Cross-vein <i>ia₁</i> :—A. Present in both wings. B. Present in hindwing only. C. Absent from both wings. | A or B. | B. | C. | B or C. | C. |
| (19) | Cross-veins <i>sa</i> in forewing and <i>ia₂</i> in hindwing:—A. Both present. B. Only <i>ia₂</i> present. C. Both absent. | B. | A or B. | C. | C. | C. |
| (20) | Shape of wing:—A. Original elongate form, as in <i>Belmontia</i> or <i>Rhyacophila</i> . B. Symmetrical, sharply pointed wing. C. With narrow base and broad termen. | B. | A. | B. | C. | A. |
| Percentage of archetypic characters present*. | | 72.5 | 62.5 | 17.5 | 60.0 | 37.5 |

*In calculating these percentages, an archaic character present in one wing only, as (2), (3), B, etc., is allowed for as one-half the complete archaic character.

*Note on the Evidence concerning the Existence of vein M_4
in the Lepidoptera.*

The evidence for the existence of M_4 in the Lepidoptera is not absolutely conclusive, as will be readily gathered from the account of my researches on the *Hepialidae*. The alternative is that the vein here taken to be M_4 is in reality the cross-vein *m-cu*. In the present state of our knowledge, it is impossible to decide finally what is the true state of affairs. My reasons for accepting the presence of M_4 , as I have done throughout Sections vi. and xiv., is that the new evidence brought forward in this research seems to me more in favour of that view than the other. The absence of a trachea M_4 in the pupal wing seemed to me for a long time to be almost conclusively against the existence of M_4 in the Lepidoptera. But the small, though very definite, trachea which I found in a pupal wing of *Xyleutes* (Text-fig. 56) tells against this; and it has to be remembered that comparatively *very few* dissections of pupal wings of archaic Lepidoptera have yet been carried out. If the trachea M_4 is present in only 1 per cent. of the wings of *Hepialidae* or *Cossidae*, its existence will nevertheless be a much stronger argument in favour of the presence of vein M_4 than is its absence from the other 99 per cent. for the cross-vein alternative. For it has now to be borne in mind that the existence of vein M_5 could *never* have been proved without the discovery of *Belmontia* or some similar fossil; seeing that, in this case also, trachea M_5 is absent from the early pupal wing, and in most cases, as with M_4 , the vein M_5 is reduced to the semblance of a cross-vein.

But there are other strong reasons why the presence of M_4 should be accepted, on the balance of evidence at present. The fossil *Archipanorpa* (Text-fig. 57) shows us a type in which M_4 is reduced to the transverse condition, so that, at first sight, it would appear to be undoubtedly a cross-vein. Yet not only the presence of strong macrotrichia upon it, but also the fact that its fusion with Cu_{1a} is incomplete,—so that it separates from this latter vein further distad, and runs freely to the wing-border,—both prove that it is a main vein in this fossil.

Again, what are we to make of the now famous individual of *Sthenopsis*, in which the same state of partial fusion is shown in the hindwing (Text-fig. 55*b*, and Comstock, 15, fig. 337) if we will not accept this conclusion? If the upper arm of the Y-

vein in this case is the cross-vein *m-cu*, then it must follow that Cu_{1a} is itself a forked vein; for neither of the branches of the terminal fork can belong to M_4 on this supposition. I do not think that anybody will accept this alternative, and I am unable to suggest any other possible explanation.

The position seems to be this:—that the evidence for the existence of M_4 in the Lepidoptera is not conclusive, but may be accepted provisionally upon the balance of probabilities. The evidence in favour of the cross-vein theory is as complete as it is ever likely to be. But those who support the theory that M_4 is present have all the possibilities of new evidence to count upon, both from further dissections of pupal wings, and from new fossil discoveries which may reinforce the evidence of *Archipanorpa* and *Sthenopis*.

In my researches upon the *Jugo-frenata* (27), I used the notation *m-cu* for the vein which I here call M_4 . The evidence from the pupal wings of *Eriocrania*, on which the notation of that paper is based, is against the presence of M_4 , seeing that there is no trachea preceding this vein in the pupal wing. The alteration in the present paper is due to the consideration of much evidence from outside the *Jugo-frenata*. I should like also to point out that, in both fore and hindwings of the *Micropterygidae* and *Mnesarchaeidae*, and also in the hindwings of the *Eriocraniidae*, the position of this vein is such that it is much more likely to be M_4 than *m-cu*, seeing that the latter, in the Order Trichoptera, is situated either at, or a little basad from, the secondary median fork. *mf'*. Only in the forewings of the *Eriocraniidae* is the position of this vein such that it would naturally be taken for *m-cu*.

A slight correction is necessary in Text-figs. 5 and 6 of the paper here referred to, (27). The dotted line passing transversely from the secondary radial fork *rf'*, to the media below it, should be omitted, since there is no cross-vein in this position.

Throughout Section xiv., the lettering of the Text-figures has been made on the view that M_4 is present, not only in the *Hepialidae*, but also in the rest of the Homoneura, and throughout the Heteroneura. The evidence from the pupal wing of *Xyleutes* (Text-fig. 56) favours this view for the Heteroneura; but, even without that, there can be no doubt that the vein which I have labelled M_4 in the *Prototheoridae* (Text-fig. 83) is the homologue of the vein labelled M_4 in the Heteroneura.

Hence the terminology M_4 must either be accepted throughout the Order, or else it must be altered throughout to *m-cu*.

It is left optional for anybody, who prefers this latter alternative, to reject the account given of the structure and evolution of the Distal Y-vein in Section vi., and to alter the Tables on pp. 650, 706, to suit the new view. The net results of the alteration would be that the *Hepialidae* would have to be regarded as somewhat more highly specialised, the *Jugo-frenata* slightly more archaic, than the percentages in Table iii. would indicate; and also that the Lepidoptera, as a whole, would be brought slightly nearer to the Trichoptera, seeing that the condition of *M* in both wings of the former will then become the same as that in the hindwing of this latter Order.

Suborder **Heteroneura.**

The problem of the evolution of the Heteroneura is a most fascinating one, and vitally concerns us here, in so far as it must be quite evident that no single existing family of the Homoneura at the present day can possibly represent the original stem of the Lepidoptera, from which both Homoneura and Heteroneura, as we know them to-day, arose. All we can be certain of is this:—that the *Heteroneura* are derived from a *Homoneurous* ancestor of which no completely generalised descendant exists to-day. The task of determining the characters of that ancestor is only to be undertaken by a careful examination of all archaic existing types, together with any fossils known; and the Archetype of the Order must be that type which combines in itself all the archaic features of this ancestor, as well as those of the Homoneura.

That being so, it is necessary here to examine carefully the following groups: (i.) the Jurassic fossil family *Palaeontinidae*, (ii.) the *Cossidae*, (iii.) the superfamily Tortricina, (iv.) the superfamily Tineina, (v.) the *Castniidae*, (vi.) the superfamily Psychina, and (vii.) the superfamily Pyralidina. To these I have added the Butterflies, whose phylogeny is a fascinating problem of its own, as yet unsolved.

The publication of Dr. A. J. Turner's paper on the venation of the *Cossidae* (32) marks a great advance in our knowledge of the phylogeny of the Heteroneura, and I shall not hesitate to refer to it whenever necessary, especially as a previous paper of my own (13) helped to stimulate Dr. Turner in his work, and as this author adopted the main contentions made

in it. It will be seen, however, in the course of the present research, that both my previous paper and Dr. Turner's came to certain conclusions which were unwarranted; in my own case, owing to lack of prolonged study of the Order, in Dr. Turner's, inevitably because he confined himself entirely to the imaginal wing-venation, by means of which it is practically impossible to arrive at the truth with regard to certain points. Dr. Turner's paper is of the utmost value, not only because of the detailed comparison of the venations of all the known genera within the *Cossidae*, but also because of the extension of the same method to selected types from all the older families, and because of his definition of the hypothetical ancestors of the Heteroneura, which he calls the family *Protocossidae*,—a name which I shall adopt here. It will therefore not be necessary for me to pass in review a large number of genera, but simply to deal, as far as possible, with those in which I have been able to study the pupal tracheation, and then to compare my results with those obtained by Dr. Turner, by his comparative study of the imaginal venations only.

Family PALÆONTINIDÆ (Fossils only).

In Text-fig. 84, I have reproduced from Handlirsch (2, Atlas, plates xlix., l.) a number of his figures of the best preserved of these fossils. The first of these Jurassic insects to be discovered, and one of the oldest in actual horizon, was *Palæontina oolitica* Butler (Text-fig. 84, f), of which, unfortunately, only the forewing is known. Another interesting type known only from its forewing is *Palæocossus jurassicus* Opp. (Text-fig. 84, a). Besides these, I have figured four genera in which the fore and hindwings are both fairly well preserved. Whether Handlirsch's restorations, which I have reproduced herewith, are correct in every detail, may be a matter of individual opinion. I can only say that, after examining the photographs of the fossils which he also publishes, I cannot see any definite errors in the restorations, though it is perhaps doubtful how far he is justified in restoring the subcosta and radius of the forewings of some of the types on the somewhat abnormal plan that he has sometimes adopted. What is absolutely certain is that those fossils in which the hindwing is preserved were *most certainly not Homoneura*. The hindwings are reduced in size to a level rarely attained, even in highly specialised Hetero-

neura of to-day; and the reduction in the number of veins is quite obvious also. It is, therefore, necessary to study, first of all, those types in which the hindwings have been preserved. We shall then be able to compare the *forewings* of those types with the isolated forewings of *Palaeontina* and *Palaeocossus*, in order to determine whether these two latter genera are related to them, or whether, perhaps, they may not be regarded as true Homoneura, not related to the rest.

First of all, then, we must make a comparison of the four hindwings shown, and note the points common to all in Handlirsch's restorations. They all agree in one very remarkable character, viz. that the media is reduced to a single straight vein. As far as I can see, from the photographs given by Handlirsch, there is no doubt on this point. Rs is two-branched in every case; so that it is clear that its two branches may be named R_{2+3} and R_{4+5} respectively. R_1 is present in all; and in at least one case a perfectly separate Sc is also present (*Limacodites*). Cu is three-branched in all cases; and one naturally concludes that these three branches are the homologues of the three branches existing in the Order to-day. (But it may be noted that it would be possible to interpret the vein marked 1A in *Limacodites* as Cu_2 in which case the vein marked Cu_{1a} must be a branch of M captured by Cu^1 , as may be seen in many highly specialised forms existing to-day.

The hindwing of the *Palaeontinidae*, then, had the following veins present:—Sc (? sometimes absent), R_1 , R_{2+3} , R_{4+5} , M, Cu_{1a} , Cu_{1b} , Cu_2 , 1A, 2A (? sometimes absent). This is a possible total of ten veins at the most, out of the thirteen or fourteen that should be present in a truly Homoneurous hindwing. Thus the conclusion is arrived at that the *Palaeontinidae* whose hindwings are preserved are *not Homoneura*.

They must therefore be either (a) Heteroneura derived from the same stem as those of the present day, or (b) Heteroneurous forms derived from the original Homoneurous stem by an entirely separate line of descent.

Now, as we shall see in our examination of recent Heteroneurous types below, these latter have all been evolved along a single line of descent, from what Turner has called the *Protocossid* ancestral type (32). The method of reduction, in the evolution of that type, has been solely by loss of the branches of Rs, and not by loss of the branches of M. Further,

in those highly specialised types in which, after Rs has already become simplified, further reduction leads to loss of branches of M in the hindwing, the main stem of M is always obliterated. Thus there are no known types within the existing Heteroneura which reproduce the condition of the hindwing of the *Palaeontinidae*.

The only conclusion that I can come to is that, although the *Palaeontinidae* in which the hindwings have been preserved are most certainly Heteroneurous, they do not belong to the line of descent from which all our present-day Heteroneura are derived. They must be considered as a separate offshoot from the Homoneura, specialised by reduction of the branches of M in the hindwing, and therefore having left no descendants at the present day, and with no near relatives amongst present-day Heteroneura. Handlirsch, therefore, in arguing in favour of a relationship between these moths and the *Limacodidae* (2, p. 619), is not on firm ground, and his contention should be abandoned.

We may now return to the study of the family, and consider whether the venation of the *forewings* of those genera in which the hindwings are preserved is sufficiently near to those in which they are not, to justify us in accepting Handlirsch's placing of them all as closely related types.

The answer to this question must undoubtedly be in the affirmative, for the following reasons:—

(1) All the fossil types agree in having the branches of M in the forewing occupying the middle distal portion of the wing, whereas the branches of Rs are crowded up anteriorly, as in the higher Heteroneura of the present day. If we compare this with the condition to be seen in the *Hepialidae* (Text-figs. 81, 82), we see how little justification there is for Meyrick's assertion that "there is little doubt that it (i.e. *Palaeontina oolitica*) belongs to the *Hepialidae*" (17). The forewing of *Palaeontina* is particularly close, in this and most other respects, to that of *Prolystra lithographica* Opp. (Text-fig. 84, d), one of the forms in which the hindwing is preserved.

(2) As regards the condition of M_4 , there is a gradation from the oblique position, such as is found in the *Hepialidae*, through the intermediate condition seen in *Palaeontina*, to the transverse position seen in *Limacodites* (b) and *Prolystra* (d). Of all the forms figured, the most archaic condition of M_4 is to be seen in

Eocicada (c) which, in the extreme reduction of its hindwing, is the most heteroneurous form of all.

(3) As regards the manner of branching of Rs in the forewing, this comes closest to that of the *Hepialidae* in *Prolystra* and *Palaeontina*; but in the former of these R_1 is missing, and in the latter it is much reduced. Both, then, stand in advance of the *Hepialidae*. In the other genera, the method of branching of Rs, if correctly restored, is highly specialised, and most certainly not of the Hepialid type.

(4) In the forewings of all the genera, Cu_2 is a complete vein, whereas it is reduced in *Hepialidae*. Further, *Eocicada* shows the unique specialisation of having Cu_2 moved distad beyond the secondary cubital fork, an extraordinary character which at once places this genus as far removed from any existing type of Lepidoptera.

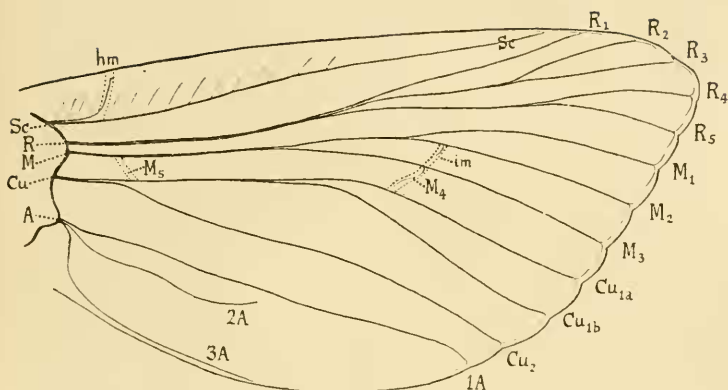
The forewing of *Palaeocossus* (Text-fig. 84, a) seems about as closely allied to that of *Prolystra* (d) as is that of *Palaeontina*; but it differs from both these latter in having lost the original dichotomic manner of branching of Rs.

To sum up, then, it would appear that the Jurassic *Palaeontinidae* form either a family, or a group of allied families, of distinct heteroneurous venational type, but not related to any existing Heteroneura. They are best regarded as a special line of development from the old Homoneurous stem of the Order, which have died out without leaving any direct descendants at the present day. They should not be included in the Heteroneura as at present defined, but may be regarded as an isolated side-branch, under the name Palæontinoidea.

Family COSSIDÆ.

This family includes both the *Zeuzeridae* and the *Cossidae* (or *Trypanidae*) of some authors. Turner has done a valuable service in establishing the essential unity of these two groups, which Meyrick, for instance (3), placed widely apart on very insufficient grounds. The venational schemes of all the known genera are figured in Turner's fine paper (32).

For the study of this family, I have to thank Mr. Luke Gallard for a large supply of larvæ of the two genera *Xyleutes* and *Culama*. Unfortunately I did not succeed in keeping any of the latter alive until they pupated, although I had them for



Text-Fig. 85.

Tracheation of forewing of freshly formed pupa of *Xyleutes eucalypti* (Scott). (x 3.3). Lettering as on p. 535.

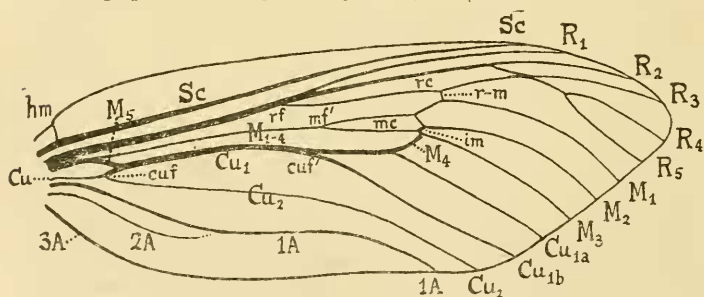
some months. Of the former I obtained and dissected several pupæ, with very interesting results.

Text-fig. 85 shows the tracheation of the forewing of a pupa only a day or two old. The resemblance of this wing to that of the *Hepialidae* is very striking, and is the more noteworthy when we consider how very different the imaginal forewings of these two families appear. Comparing *Xyleutes* with *Leto* (Text-fig. 80), we note that the tendency towards the splitting-back of the tracheæ is much more marked in the latter (and in all *Hepialidae*), and that the former is the more archaic in having trachea Cu_2 of full length. The subeostal veinlet is supplied, in both forms, by a special trachea arising alongside Sc. In *Xyleutes* there is a well-marked series of branch-tracheæ arising from Se and proceeding towards the costal border. Similar tracheæ can be seen in the pupæ of many large Lepidoptera, but in none are they so well developed as in this family. I have figured them here in order to call attention to the obvious fact that, if veins were to be formed over the courses of these tracheæ, there would result the original condition of a complete set of costal veinlets, such as has been preserved in the Megaloptera and Planipennia at the present day. As long as these tracheæ still exist in the pupæ of Lepidoptera, can anyone deny the possibility of the evolution of a new line, in

which these costal veinlets might be restored in their entirety; supposing that some other change, such as loss of scales in a clear-winged form, might make such a restoration of value to the species?

The forewings of *Xyleutes* and the *Hepialidae* also agree in the absence of the cross-vein *ir* and the presence of *im*. But they differ in the details of the forking of Rs. In *Hepialidae*, the original condition seen in *Belmontia* (Text-fig. 63) and all archaic Trichoptera is retained, viz., that R_{4+5} forks close to rf' , R_{2+3} much more distad from it. In *Xyleutes*, the latter trachea forks at a level slightly nearer rf' than does the former; and this difference is greatly increased in the imaginal venation (Text-fig. 86). In the pupal wing of *Xyleutes*, rf' lies only just distad from rf ; but Rs remains separate from R_1 , though very close to it. In the imaginal wing, a slight fusion of the basal part of Rs with R_1 takes place, resulting in the appearance of R_{2+3} and R_{4+5} arising as slightly separated from one another upon R_1 . This formation is of great interest, since it is a very clear illustration of the manner in which *two apparent radial sectors* can be evolved from the original single one. Similar formations may be seen in many families of Lepidoptera; and, in some cases, notably the Butterflies, the change has extended to the pupal tracheation, and has become a fixed character there. Carried to its fullest extreme, the same character may be seen in the pupal and imaginal wings of the family *Hemerobiidae* (Order Planipennia).

In the pupal forewing of *Xyleutes*, R_{2+3} and R_{4+5} remain



Text-Fig. 86.

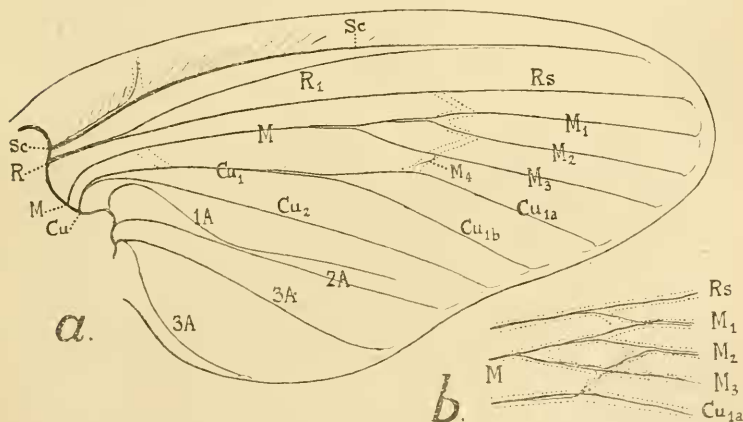
Venation of forewing of *Xyleutes eucalypti* (Scott), imago (x 0.8).
Lettering as on p. 535.

separate throughout their lengths. In the corresponding imaginal wing, the radial cell or aerole (*re*) becomes closed distally by a slight fusion of R_{4+5} with R_3 (Text-fig. 86). The original method of fusion of this cell, by means of the cross-vein *ir* (absent in *Xyleutes*) is still to be seen in the more archaic Cossid genus *Macrocyttara* (Turner, 32, p. 169, fig. 22), but this genus has R_{2+3} and R_{4+5} arising more widely apart from R_1 than in *Xyleutes*.

The vein M_5 appears early in the pupal wing of *Xyleutes*, and a trachea of great strength grows out into it either in late pupal life or at metamorphosis. In the imago, this vein remains primitive, in so far as it is not completely aligned with Cu_1 ; it also becomes of immense size in comparison with the weak main stem of Cu below it (Text-fig. 86). Cu_2 remains a complete vein, though not strongly formed; and the small basal piece of Cu_1 is clearly to be seen as a fairly strong vein.

In one pupa which I dissected, a very definite trachea M_4 was found in both wings. This formation is figured and discussed more fully in Section vi., p. 586. The other changes in the regions of M, Cu and the anal veins can be easily gathered by comparing Text-figs. 85 and 86.

The pupal hindwing of *Xyleutes* (Text-fig. 87) differs, of



Text-Fig. 87.

Tracheation of *a*, hindwing of freshly formed pupa of *Xyleutes eucalypti* (Scott). (x 3.3); *b*, tracheation in the region of the discocellulars, in a more advanced pupa. Lettering as on p. 535.

course, very materially from that of the *Hepialidae*. The essential points to be noted are the following:—

(1) R_1 gradually approaches the stronger trachea Sc , and fuses with it distally. The result, in the imago, is the formation of a single strong vein $Sc+R_1$ distally, continuing the line of Sc basally; while the basal part of R_1 itself appears as an oblique vein considerably shorter in length than its corresponding trachea in the pupa. Thus "vein 8" of systematic Lepidopterists is proved to be a composite vein, $Sc+R_1^*$; and I was in error in my previous paper (13) in calling this R_1 . It should be noted that, while this formation is to be found in the hindwings of *all* Heteroneura, nevertheless the share taken in the formation of the vein $Sc+R_1$ by its two components differs very greatly in different families; see, for instance, *Wingia* (Text-fig. 90), in which R_1 is dominant, and *Euschemon* (Text-fig. 99), in which Sc is dominant.

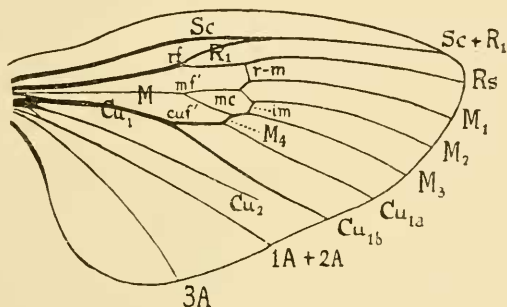
(2) Rs is a single unbranched trachea. This is the condition to be found in the early pupæ of all the older Heteroneurous types. Later on in pupal life, it frequently happens, as in *Xyleutes* itself (Text-fig. 87, *b*), that a trachea of small calibre grows out from Rs towards M_1 , traversing the cross-vein $r-m$. This is correlated with the outgrowth of other tracheæ along the cross-vein im and the vein M_4 , so that the zig-zag veins that are destined to form the distal termination of the basal cell (called collectively the *discocellulars*) become well supplied with tracheæ, by invasion of the region of M both above from Rs and below from Cu_{1a} .

(3) $1A$ loops up strongly towards Cu_2 , but does not quite succeed in fusing with it. The condition is, however, very similar to that seen in the Homoneura, and the failure to complete the fusion may well be due to the very evident increased breadth of the anal area in this wing. In the narrower wing of *Wingia* (Text-fig. 90), the fusion is completed.

(4) After diverging from Cu_2 , $1A$ approaches $2A$ towards the middle of its length, and fuses with it for a short distance, afterwards becoming of weak calibre, diverging slightly away from $2A$, and failing to reach the wing-border. The result of this, in the imaginal venation (Text-fig. 88) is a small basal Y-vein formation, not easy to make out in *Xyleutes*, but evi-

*This specialisation was pointed out by Comstock and Needham as long ago as 1899 (14).

dently closely analogous to the single anal loop or Y-vein of the forewings. It is, however, important to notice that, in the forewing, 1A is the dominant member of the Y-vein, while 2A is reduced. In the hindwing, the reverse is the case. The importance of this formation lies in the fact that it occurs throughout the Superfamily Tortricina, and thus affords a striking proof of the very direct descent of that group from the base of the



Text-Fig. 88.

Venation of hindwing of *Xyleutes eucalypti* (Scott). (x 0.8). Lettering as on p. 535.

Cossid stem. This small basal Y-vein is also to be seen in a few Tineina (*Taleporia*, *Adela*, *Wingia*, *Acompsia*), in the *Castniidae* and *Thyrididae*, but is eliminated in the majority of the Tineina and Pyralidina, as well as from all the Psychina and the Butterflies.

At metamorphosis, there is a great increase in the calibre of the veins at the base of the wing. The basal formations, such as M_5 , the approach of 1A to Cu_2 , and the fusion of 1A with 2A, become withdrawn very close to the actual wing-base, and partially lost in the copious deposition of vein-chitin there laid down. An examination of the underside of a carefully de-sealed wing is necessary to reveal their presence. It will be seen that, in most Heteroneura, the presence of these archaic formations becomes more and more masked as specialisation proceeds, until they become practically obliterated in the higher groups, first in the hindwing, in which they are never so conspicuously developed as in the fore, and then in the latter also.

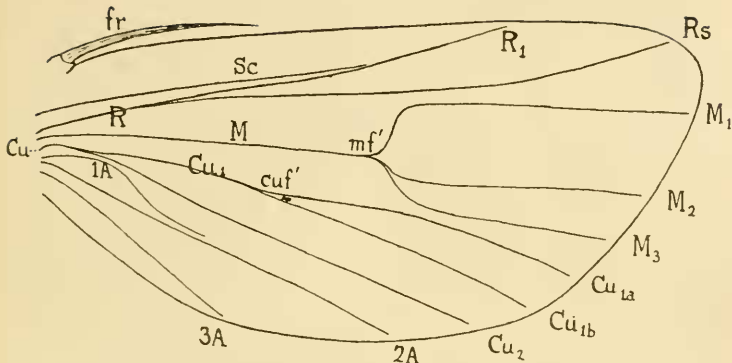
Superfamily TORTRICINA.

The Codlin-moth, *Carpocapsa pomonella* (Linn.) afforded me a plentiful supply of pupæ for this group. The pupa being small, and the wings delicate, the dissections were not at all easy.

The basal tracheation of the pupal forewing is shown in Plate xxxiv., fig. 22. It differs very little from that of *Wingia* (Text-fig. 90), so that there is no need to figure the whole wing separately. The principal differences are that, in the forewing of *Carpocapsa*, the stem of R_{4+5} persists at metamorphosis, so that the basal cell and radial cell or areole remain separate (a more archaic condition than that seen in *Wingia*); that Cu approaches basally so close to M that the formation of the separate vein M_5 is prevented (in *Wingia*, the formation of this vein can just be made out in the early pupa); and that there is no kink in 1A at the point where 2A fuses with it.

In discussing the evolution of the cubito-median Y-vein (Section iii.), it was pointed out how all the successive stages of specialisation, leading to the obliteration of M_5 , and finally to a definite fusion between Cu_1 and M_{1-4} , could be seen in a single Order, or even in a single family, such as the *Rhyacophilidae*. The same line of advance is here made evident within the Heteroneura, the stage shown in *Carpocapsa* being closely equivalent to that indicated as the last stage (Text-fig. 42 d) in the Order Trichoptera. But there is one important difference, viz. that the fusion in *Carpocapsa* takes place, not between M_{1-4} and Cu_1 , but between M_{1-4} and the main stem of Cu. This is not due to any movement of the cubital fork distad, for it is quite evident that this fork itself is migrating basad (and, indeed, in many advanced Heteroneura, trachea Cu_2 may be so far split back from Cu_1 as to originate separately from it on the alar trunk); but it is due to the general tendency for the basal formations as a whole to move closer to the base of the wing in this Suborder, and is part of the whole line of evolution by which, in the end, all those basal specialisations which no longer serve any useful purpose become obliterated.

The tracheation of the pupal hindwing of *Carpocapsa* is shown in Text-fig. 89, for the special purpose of illustrating (a) the dominance of R_1 over Sc, as in the Tineina, and (b) the further weakening of 1A, and the dominance of 2A in the formation of the anal Y-vein. We may note also the close



Text-Fig.89.

Tracheation of pupal hindwing of *Carpocapsa pomonella* (Linn.), showing weakened condition of 1A. (x 25). Lettering as on p.535.

approximation of trachea M_3 to trachea Cu_{1a} , resulting in the complete obliteration of the remnant of M_4 between them, and the association of the two corresponding veins together, as connate veins arising from the lower angle of the cell in the imaginal hindwing.

As I have made a very complete study of the obliteration of the main stem of M in the case of *Wingia* (see below, p. 669), it is only necessary to say here that *Carpocapsa* agrees with *Wingia* in this and many other respects, which need not be detailed here.

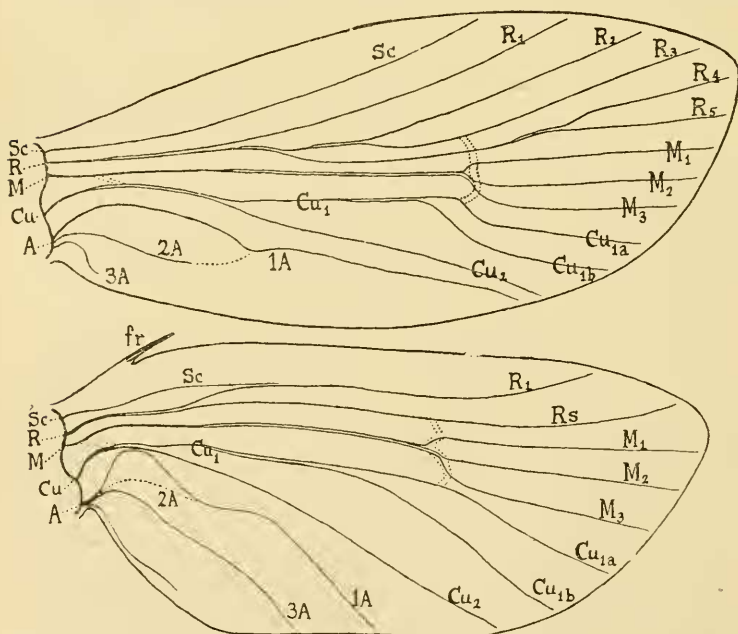
In the imaginal forewing the course of Cu_2 is barely indicated, while in the hindwing it is very weakly chitinised. The tendency throughout the Suborder is for this weak concave vein to become, firstly a mere furrow or groove, without definite chitinisation, and then to be completely eliminated. Contrast *Wingia* (Text-figs. 90, 93), which is more archaic than *Carpocapsa* in this respect, with *Euschemon* (Text-figs. 99, 100), which is more specialised.

The descent of the Tortricina from a Cossid-like ancestor is, I think, very obvious. But, since all those Tortricina, in which the radial cell (areole) is closed, have the closure brought about in the most archaic manner, viz. by the interpolation of the cross-vein *ir*, it is clear that the group is not, as a whole, derivable directly from the *Cossidae*, but rather from Turner's hypothetical ancestral family *Protocossidae*.

Superfamily TINEINA.

In this great group, thanks to the kindness of my friend, Mr. G. Lyell, I was well supplied with pupæ, especially in the cases of the more archaic families *Plutellidae* and *Oecophoridae*. A large number of pupæ belonging to the genera *Wingia*, *Coesyra*, *Heliocausta*, *Cebysa* and *Tinea* were dissected. In the case of *Wingia lambertiella*, Mr. Lyell supplied me with a very long series of well-fed larvæ, and pupæ in all stages; so that I was able to study, in this species, the changes that take place during pupal life, and at metamorphosis, in greater detail than in any other case.

This beautiful moth belongs to the family *Oecophoridae*; its larvæ spin the leaves of Eucalypts together, and pupate inside a thick, white, silken web or tunnel.



Text-Fig. 90.

Tracheation of wings of freshly formed pupa of *Wingia lambertiella* (Wing.), (fam. *Oecophoridae*), (x 8). Lettering as on p. 535.

Text-fig. 90 shows the tracheation in the wings of a freshly turned pupa of *Wingia*. These wings are very delicate, and, being somewhat small, require very careful dissection. Later in pupal life, they become very tough, and can be easily removed from their sheaths without any damage. The late pupal wing can be cleared in chloro-phenol, the tracheæ remaining unshrivelled for some time, even under this strong reagent.

The points to be noted in the early pupal wings are as follows:—

(1) Trachea M is far removed from trachea Cu at its origin, and belongs properly to the costo-radial group.

(2) The three anal tracheæ come off close together in a bunch, far removed from Cu.

(3) All the branch tracheæ are split back very far towards the bases of the main tracheæ to which they belong, so that the actual point of origin of any given branch trachea is situated very much further basad than is the true fork which corresponds to it in the imaginal venation. (This character is to be noted in all Lepidopterous pupæ, to a greater or less extent, but is particularly marked here.)

(4) R_{2+3} divides near the middle of the wing, R_{4+5} much further distad. In the *Hepialidae*, the reverse is the case, as also in the Trichoptera.

(5) M and Cu_2 are complete tracheæ, not reduced in either wing.

(6) In forewing, there is a kink in the course of 1A, indicating the point at which, in the imaginal venation, 2A will loop up with 1A. But trachea 2A does not reach this point, as it stops considerably short of it.

(7) In hindwing, Rs is a simple trachea, and Sc is much reduced, its distal end lying close alongside R_1 .

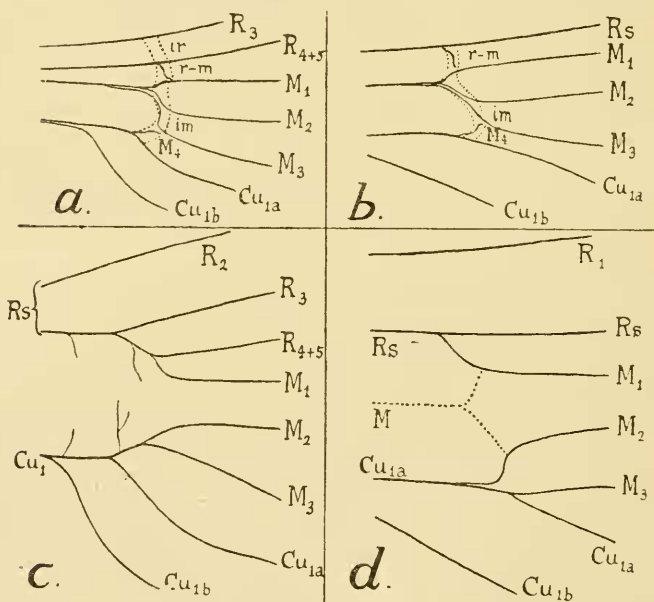
(8) In hindwing, 1A makes a large upward loop, so as to come into contact with Cu_2 not far from its origin. (Compare the condition of these two tracheæ in *Hepialidae*.)

(9) In hindwing, trachea 2A is aborted, the course of the vein in the imaginal wing being indicated only by a pale band, represented by a dotted line in Text-fig. 90.

In Text-fig. 90, I have indicated by dotted lines the positions of M_5 , the distal closure of the basal cell, and the completion of the looping-up of 2A on to 1A, although these are not clearly apparent until the pupa is more than a day old. They

arise as part of the pale banding which foreshadows the imaginal venation.

The principal changes which take place during pupal life are those which affect the *discocellulars*, at the distal end of the basal cell. Text-fig. 91 shows the condition in a pupa ten days old. A small trachea grows out from R_{4+5} in forewing, or R_s in hindwing, down towards M_1 , while another grows out from Cu_{1a} up towards M_3 . Just before metamorphosis, these tracheae are still only quite small. But, during metamorphosis, they capture the respective tracheae towards which they have been growing; so that, in the freshly-emerged imaginal wing, as soon as it is fully expanded, the condition is that shown in Text-fig. 91, *c*, *d*. Thus M_1 becomes completely hitched on to



Text-Fig.91.

Details of the changes in the tracheation in the wings of *Wingia lambertiella* (Wing), (fam. *Oecophoridae*) in the region of the discocellulars; *a*, forewing, *b*, hindwing, of late pupal stage; *c*, forewing, *d*, hindwing, of freshly emerged imago. (x 15). Lettering as on p.535.

R_{4+5} in forewing, or R_s in hindwing, at metamorphosis; while M_3 likewise becomes hitched on to Cu_{1a} .

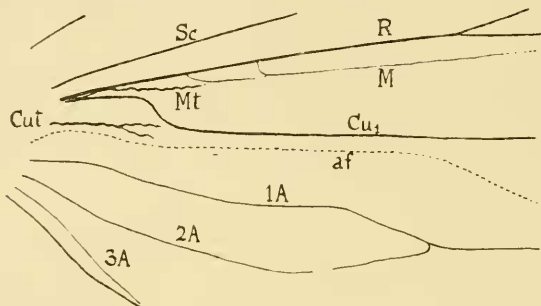
Moreover, the whole of trachea M becomes aborted at metamorphosis, so that M_2 is cut off from its original source of supply. In the fresh imaginal wing, this trachea is seen to have become hitched on to M_3 in the forewing, but on to Cu_{1a} in hindwing. This must evidently be effected by the outgrowth of a small trachea such as that which captured M_3 , though this outgrowth did not begin to appear in the late pupa, and must have developed during metamorphosis.

The final result, in the forewing, is that no part of the true main stem of M , either trachea or vein, is visible at all. In the hindwing, however, a delicate groove indicates the position of M , together with its forking into two distally. This is shown by a dotted line in Text-fig. 91, *d*.

A further remarkable change at metamorphosis is the complete abortion of the stem of R_{4+5} , both trachea and vein, in the forewing, as far as the inter-radial cross-vein *ir*, which is present in *Wingia*, as also in *Carpocapsa* and all archaic Tortricina and Tineina. The manner in which this is brought about can be seen from Text-figs. 91, *a*, *b*. It has already been mentioned that, during pupal life, a small trachea grows out from R_{4+5} in the forewing towards M_1 . This small trachea traverses the cross-vein *r-m*, which appears quite early in pupal life, with the rest of the imaginal venation. Above this cross-vein, and in line with it, the cross-vein *ir* is also to be seen in the pupal wing, and it is this cross-vein which furnishes the channel for the greater change at metamorphosis. For, at that time, a further trachea grows out from R_3 along *ir*, and captures both R_{4+5} and its already attached M_1 ; while, at the same time, the trachea R_{4+5} , basad from *ir*, shrivels up.—the final result being as shown in Text-fig. 91, *c*.

Turner (32, p. 172) has already pointed out, from a study of the imaginal venation only in the Tortricina, that the large basal cell is really a composite structure, formed from both the true basal cell and the areole or radial cell; to this composite cell he has given the name *areocel*; while the basal part of R_{4+5} , which separates the true basal cell from the areole, and by the elimination of which the areocel is formed, is called by him the *chorda*. What he has failed to emphasise is the fact that the cross-vein *ir* is present, and forms the boundary of the

areocel between R_3 and R_{4+5} (in *Wingia*), or, in those cases where the latter is not stalked beyond the areocel, between R_3 and R_4 (as in *Carpocapsa*). Unless this cross-vein had been present, to furnish the channel along which the new trachea grew out from R_3 , no areocel could have been formed. Thus we are bound to conclude that the cross-vein *ir* was present in the ancestral forms of the Tortricina and Tineina.*

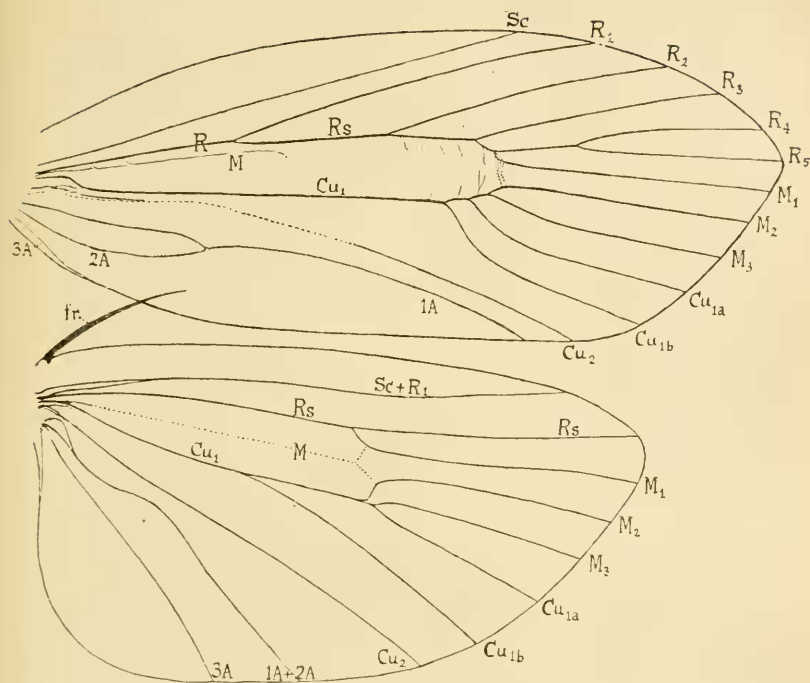


Text-Fig. 92.

Details of tracheation of the imaginal forewing, freshly emerged, of *Wingia lambertiella* (Wing), (fam. *Oecophoridae*). (x 11). Note the shrivelled median trachea (*Mt*) and cubital trachea (*Cut*). Lettering as on p. 535.

Another striking change at metamorphosis in *Wingia* is the complete and quite sudden switching off of the trachea Cu_1 near its point of origin on Cu , across to M , via M_5 . In the latest pupal wings which I examined, I could find no trace of a trachea in M_5 , though I looked carefully for it. But, in the fresh imaginal wing, a strong trachea proceeds from the base of M , curving down along M_5 (which, in this moth, is not at all well aligned with Cu_1), and supplying Cu_1 right to its ends. Above this trachea could be seen the shrivelled remnant of trachea M_{1-4} , while two much finer tracheae, proceeding from R , more or less followed the line of M distad from it (Text-fig. 92). Below M_5 , the remnant of trachea Cu was plainly visible, with its original dichotomy into Cu_1 and Cu_2 , the former still exactly in line with

*Further proof of this fact is to be found in the existence of a number of genera, in both these superfamilies, in which the areole or radial cell is retained in its entirety, and in every such case this cell is closed by *ir*. (See Turner, 32, figs. 24-30).



Text-Fig. 93.

Wingia lambertiella (Wing), (fam. *Oecophoridae*). Tracheation of freshly emerged imaginal wings. (x 6). Lettering as on p. 535.

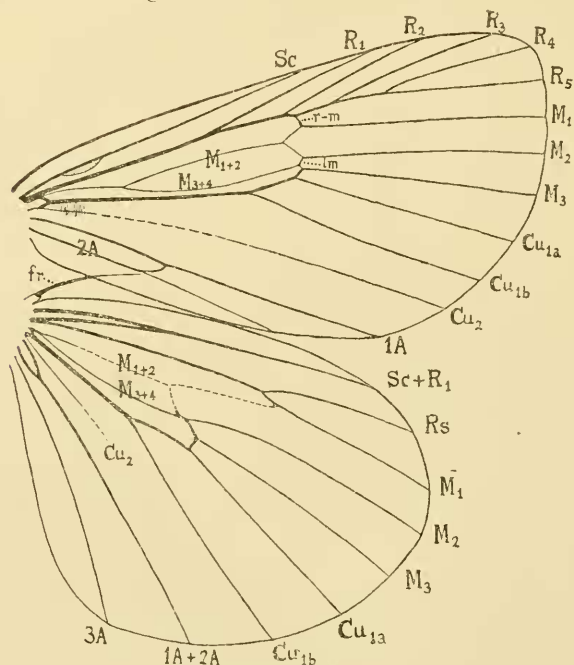
the continuation of Cu_1 beyond the bend formed by M_5 . It should also be noted that, in the forewing, Cu_2 becomes aborted through the breaking of its connection with trachea Cu . In the wing from which Text-fig. 92 was drawn, a little piece of this trachea remained near the base, and a longer piece distally. The chitination of the vein Cu_2 in both wings, and of the anal veins in the hindwing, is very weak.

In Text-fig. 93, the actual venation is omitted, the figure being intended to show the courses of the *tracheae*. The veins themselves are stout, especially Sc in forewing. They enclose all the main tracheae and their branches, and also complete the basal cell distally, and the anal loop in the forewing.

Family CASTNIIDÆ.

This family is only represented in Australia by the genus *Synemon*. The genus *Euschemon*, originally placed in it, is clearly, both from its venation and its life-history, far removed from the *Castniidae*, and will be dealt with in this Part under the *Hesperiidae*, to which it properly belongs.

Text-fig. 94 gives a diagrammatic representation of the venation of the genus *Synemon*, with all the archaic characters found in the various species included in the one figure. The very large and handsome *S. directa* Walk., from Western Australia, was found to possess the largest number of archaic features; so that its venation approaches very closely to that of the figure. In this species, however, there is no anal Y-vein in the forewing, and 2A runs separately to the wing-border, as shown by a dotted line in the figure.



Text-Fig.94.

Diagram to show venation of the genus *Synemon*, containing the more archaic features selected from several different species. Lettering as on p.535.

Great efforts were made to secure larvæ and pupæ of this genus, but were frustrated by the severe drought of last summer. My thanks are due to Mr. E. J. Dumigan for a large supply of fresh imagines of a small (undetermined) species from South Queensland, and to Mr. G. Lyell for named examples of several species, including Western Australian forms.

The pupal tracheation probably does not differ very much from the venational scheme given in Text-fig. 94. The media is complete in both wings; and, as in the *Hepialidae*, the point mf' is placed close to the base of the wing. The stalked arrangement of the branches of Rs in the forewing is a specialisation peculiar to *Synemon*; the genera *Castnia* and *Gazera* have the usual dichotomic arrangement, with the radial cell, or areole, closed by the cross-vein ir , as figured by Turner (32, p. 175). Important specialisations are to be noted in the following points:—

(1) M_5 can just be made out as a very short vein at the base of the forewing, but appears to have become completely suppressed in the hind.

(2) In both wings, M_1 has moved a considerable distance away from M_2 , and has evidently been captured by Rs, through the outgrowth of a special trachea along $r-m$. (Cf. *Wingia*, p. 669). The importance of this will become more evident when we come to consider the next two groups.

(3) In the hindwing, there is a small basal Y-vein, formed by the fusion of $1A$ and $2A$, as in *Carpocapsa* and other Tortricina.

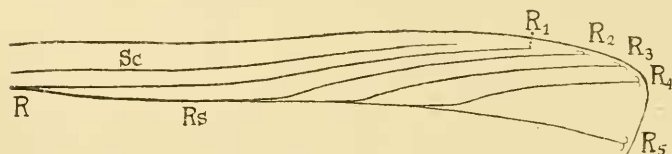
The peculiar form of the basal cell of the hindwing, which remains incomplete and of very irregular shape, is very noteworthy, and shows that this family is far more archaic than the Tortricina and Tineina in this respect.

Taking all these points into consideration, it must be clear that the conclusion of Handlirsch, Turner and others, that this family stands far apart from other Lepidoptera, and is only to be derived as an isolated line of development from the original ancestor of the Heteroneura, is fully justified. The venational scheme shows no possible avenue by which the Butterflies could have evolved from this family; and we can only conclude that the adoption of the day-flying habit, and the correlated development of clubbed antennæ, have been independently gained in the two groups.

Superfamily PSYCHINA.

We come next to a group of rather archaic Heteroneura, in which at least one main branch of M is retained within the basal cell, but the radial cell of the forewing is completely obliterated, and M_1 has become permanently attached to Rs in the hindwing, not only in the imaginal venation, but also in the pupal tracheation.

The families included in this group are the *Limacodidae*, *Zygaenidae*, *Megalopygidae* and *Psychidae*. Each family is itself specialised in a very definite direction; but I selected the *Limacodidae* as probably the most archaic, and, at the same time, the easiest (in Australia) in which to obtain plentiful supplies of pupæ. Unfortunately, out of about sixty cocoons of this family collected in 1917-18, not a single larva has so far pupated, al-



Text-Fig. 95.

Tracheation of the radial sector in pupal wing of *Doratifera longerans* (Walk.), (fam. *Limacodidae*), to show the transference of R_3 from R_{2+3} across to R_{4+5} . ($\times 10\frac{1}{2}$). Lettering as on p.535.

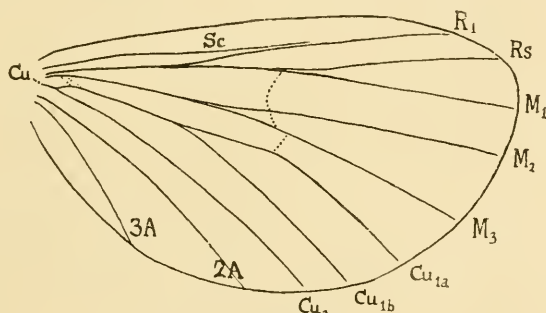
though they remain perfectly healthy within them. The reason is probably to be found in the severe drought of last summer. I have, therefore, to be content with dissections of pupæ of the genera *Doratifera* and *Apoda* made in 1917, at a period before I was fully aware of the importance of drawing the basal connections carefully.

The condition of trachea Rs in the forewing of the *Limacodidae* is shown in Text-fig. 95. It will be seen that R_3 has migrated across from R_{2+3} to R_{4+5} , thus automatically preventing the formation of the typical archaic radial cell or areole. In the imaginal venation, this new condition is preserved intact, and the point of origin of R_3 moves even further distad along R_{4+5} . As the condition of Rs in the other families of this group is closely similar to this, it will probably be found to be due to the same cause, when their pupal wings come to be examined.

Text-fig. 96 shows the hindwing of a fairly advanced pupa of

Doratifera longerans. There can be no doubt here that trachea M_1 has become permanently attached to Rs . The dotted lines indicate the position of the veins closing the basal cell in the imago. The only changes at metamorphosis are the much more complete fusion of Sc and R_1 ,—a fusion which also involves a part of the base of Rs ,—and the drawing together of the two main branches of M , so that a single vein M traverses the cell from one end to the other.

The basal Y-vein formed by $1A$ and $2A$ in the hindwing is absent in *Doratifera*. A reference to the pupal tracheation shows that this must have been brought about by abortion of



Text-Fig. 96.

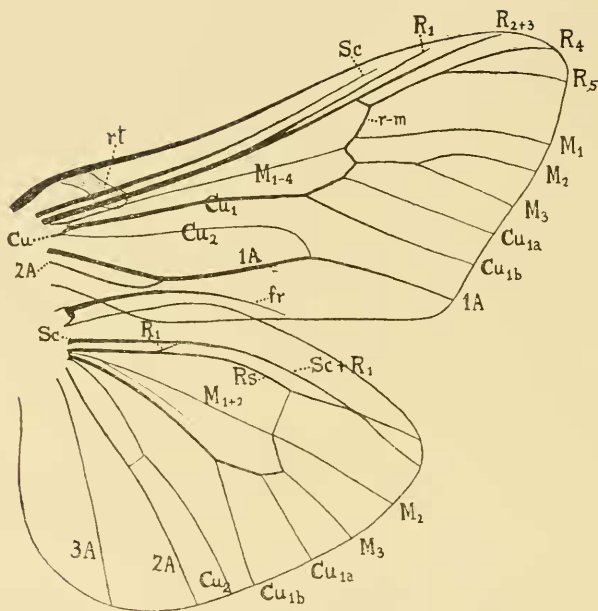
Tracheation of pupal hindwing of *Doratifera longerans* (Walk.), (fam. *Limacodidae*). ($\times 9\frac{1}{2}$). Lettering as on p. 535.

trachea and vein $1A$, since the only trachea present does not arch upwards towards Cu_2 , and must therefore be $2A$.

The tracheation of the pupal wings of *Apoda* agrees closely with the above, but trachea Sc in the hindwing is shorter.

Of the *Zygaenidae* I have, unfortunately, been unable to obtain any pupæ in a suitable state for dissection. The *Megalopygidae* do not occur in Australia. But it has been shown by many authors, without any doubt, that both these families are closely related to the *Limacodidae*; so that we may reasonably assume that the pupal tracheation will not differ very greatly from that of this latter family.

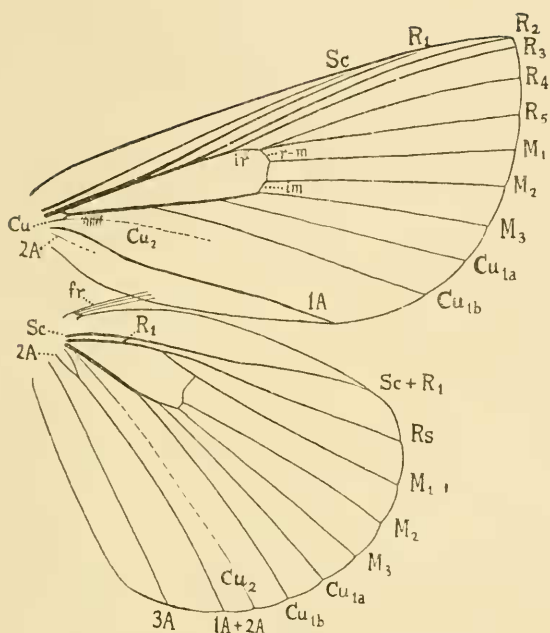
The *Psychidae* appear to be the most highly specialised family, because of their lack of scales, their extraordinary life-history, and the great differentiation between the small, swift-flying males and the huge, larviform, wingless females. The venation is correspondingly specialised, M_1 having apparently been com-



Text-Fig. 97.

Clania tenuis Rosen. (fam. *Psychidae*), imaginal venation, (x 7). Lettering as on p. 535. Note the cross-vein joining Cu_2 with 2A in hindwing, and the fusion of Cu_2 with 1A in forewing.

pletely eliminated from the hindwing; while, in the forewing, there is a unique specialisation in the form of a union of Cu^2 with 1A, well beyond the anal Y-vein. The frenulum in this family is enormous, and the retinaculum is developed from just below the thickened costa of the forewing, as shown in Text-fig. 97. In this same figure it will be seen that there is a cross-vein joining Cu_2 with 1A. If this be really the archaic *cu-a*, it is an extraordinary thing that it does not occur anywhere else in the *Lepidoptera*, and not even in other genera of the *Psychidae*, as far as I know. I have, therefore, decided to treat this formation as a unique specialisation, which will not affect the archetypic characters of the Order. It looks as if the hindwing had undergone extreme alteration of shape; and that, during the widening of the anal area, Cu_2 and 1A, probably originally more or less approximated in part, had been drawn away from one another,



Text-Fig. 98.

Rhodoneura scitaria (Walk.), (fam. *Thyrididae*), imaginal venation, (x $4\frac{1}{2}$). Lettering as on p. 535. Note the small basal Y-vein formed by 1A and 2A in hindwing.

with the formation of a cross-vein between them at the point of original greatest approximation.

Superfamily PYRALIDINA.

This group contains the *Thyrididae*, *Pyralididae* (s. lat.) and the highly specialised offshoots of the latter. Undoubtedly the most archaic family is the first-named. An attempt to obtain pupæ of the genus *Rhodoneura* from North Queensland met with no success, very little being known about the life-history of these moths. I have to thank Mr. G. Lyell for a small supply of imagines of this genus and the allied *Addaea*.

The advance made by this group over the last is very evident, in that the basal cell is now for the first time cleared of all

traces of M in both wings,* and a definite form of wing, with regularly radiating veins from the cell as a common basis of origin, is firmly established. There is a peculiarity of the *Thyrididae* which is worthy of note, viz., that the splitting back of the branch tracheæ, originally only a specialisation of the pupal wing, has reacted on the imaginal venation also, thus throwing back the origins of most of the branch veins to points nearer the base than they were in the ancestral condition. This is well seen in Text-fig. 98, and is the principal cause of the comparative shortness of the basal cell in this family and its relatives, as compared with other groups. Compare, for instance, the type of cell found in the Butterflies (Text-figs. 99-102) with that of the *Thyrididae*, and there can be no doubt which of the two comes closest to the original condition, as regards size.

In the hindwing of *Rhodoneura*, 1A and 2A are fused together very close to the base to form a small Y-vein. The vein below this is the true 3A, homologous with that of the *Cossidae* and the Tortricina.

Unfortunately I have not dissected any pupæ of *Pyralididae*, though the family is abundant enough in Australia. In attempting to keep this research down to a reasonable level, I had to confine myself to studying only the more archaic families. Having failed to obtain pupæ of the *Thyrididae*, it will now be necessary to turn to those of the *Pyralididae* for the elucidation of a very important point, viz. the manner in which the arrangement of the branches of Rs in the imaginal forewing has been brought about. This piece of research must be left for a future occasion; for, as far as I know, no descriptions of the pupal tracheation of the *Pyralididae* have yet been published.

The importance of this question is due to the fact that the relationships of the Pyralidina to the Psychina, on the one hand, and to the Butterflies on the other, depend very greatly upon the answer. For, as we have already shown on p. 674, the condition of Rs in the *Psychina* is one in which R_3 has migrated over to R_{4+5} in the pupal tracheation; and this specialisation has become even more emphasised in the imaginal venation. But, in the Butterflies, the condition of Rs in the pupal tracheation is quite different from this. As we shall show on p. 684, through-

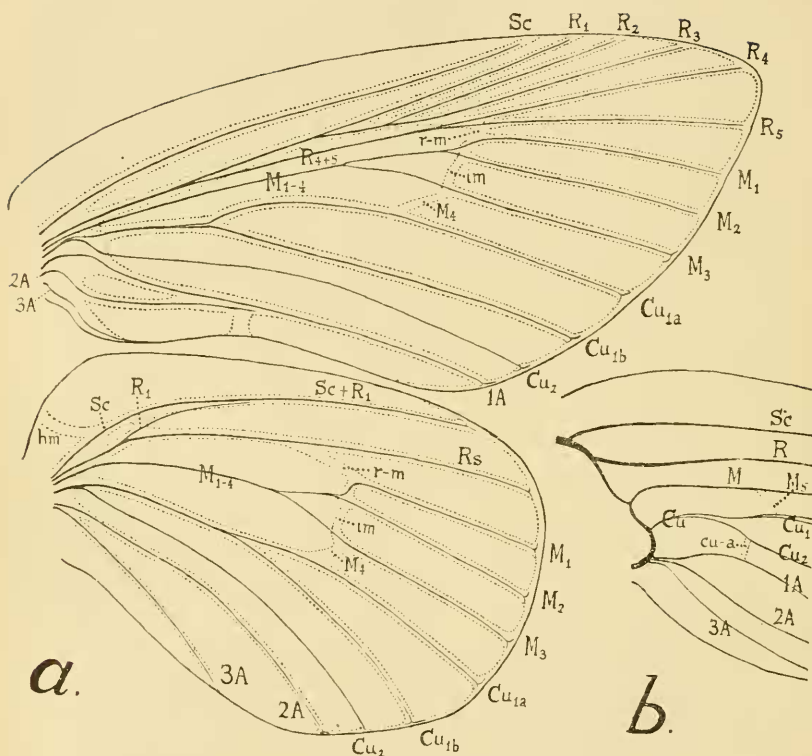
*The course of M is sometimes indicated by a faint line or groove, but is never chitinised as a true vein.

out this great group tracheæ R_{2+3} and R_{4+5} arise from the main stem of R as two *separate tracheae*, whose points of origin on R are widely distant. This is a high specialisation, in quite a different direction from that shown in the *Psychina*. But, owing to the obliteration of the chorda or main stem of R_{4+5} in the imaginal venation, the result attained in the imago is *not unlike* that to be seen in the *Psychina*, in that both groups show no *apparent* radial cell. The basal cell of the *Psychina* is merely that cell, without any additions; but the basal cell of the *Rhopalocera* is an *areocel*, formed by fusion of the radial cell or areole with the true basal cell. It will be seen from Text-fig. 98 that it is impossible to determine which of these conditions is truly present in *Rhodoneura*, and the same may be said for *Pyrilididae*.

The solution of many interesting questions rests principally on the type of Rs present in the pupal tracheation of the forewing of the *Thyrididae* and *Pyrilididae*. For there are many authors who unite the latter family (together with its highly specialised offshoots), into a single series with the *Psychina*, under the name "Pyrili-Zygæmoid Series"; though, it should be noted, they do not always include the *Thyrididae* in this same series. This latter family is placed by some in close relationship with the *Pyrilididae*, but by others it is removed far away from them, and placed close to the Tortricina. Most interesting of all is the claim made by Meyrick and Hampson that the *Thyrididae* are the ancestral group from which the Butterflies have been derived (3, p. 326). It is quite evident that the claims of the *Thyrididae* to being the ancestors of the Butterflies, and to being the close relatives of the Tortricina, on the one hand, and to the Pyrili-Zygæmoid group on the other, are in some measure conflicting. There will be no difficulty in deciding the case for the *Pyrilididae*, since pupæ of this family should easily be obtainable; but for the *Thyrididae* it is quite another matter, the family being confined to the Tropics, and very little being known about the habits of the larvæ.

The BUTTERFLIES, or Superfamily RHOPALOCERA (PAPILIONINA).

The most archaic genus in this group is certainly *Euschemon*, which stands at the very base of the family *Hesperiidae*, and is the only Butterfly in which a frenulum is present in the male. A visit was made to Port Macquarie in January of this year,



Text-Fig. 99.

Euschemon rafflesia Macleay, (fam. *Hesperiidae*), *a*, tracheation of wings of a ten-days-old pupa (x 6.7); *b*, tracheation of basal portion of forewing of a freshly formed pupa (x 10) for comparison with *a*. Lettering as on p. 535. In *a*, the pale bands foreshadowing the imaginal venation are shown as double dotted lines.

and a number of larvæ and pupæ of this rather rare insect were secured, thanks to careful directions given me by Mr. G. A. Waterhouse, who had discovered it there the previous year. The larva and pupa show definite Hesperiid characters. We shall now be able to study fully the pupal tracheation and the changes that take place at metamorphosis. The material at my

disposal was only excelled by that of *Wingia*, and I was able to study the wings at all stages of pupal life.

In order to save space in the figures, and also to show a stage different from any of those exhibited in the case of *Wingia*, I have drawn, in Text-fig. 99, *a*, both the tracheation and venation of the wings of a ten-days-old pupa. The pale bands, which foreshadow the imaginal venation proper, are indicated by the double dotted lines, each pair of which encloses a trachea, represented by a continuous black line. Alongside this figure, in Text-fig. 99, *b*, is shown the basal portion of the forewing in the freshly-turned pupa, somewhat more enlarged. From this we can see how well separated the bases of the main tracheae are at first, and how closely they tend to approximate as pupal life progresses. An exception is the group of three anal tracheae, which arise, as usual, very close together in a single bunch.

The following important points should be noted:—

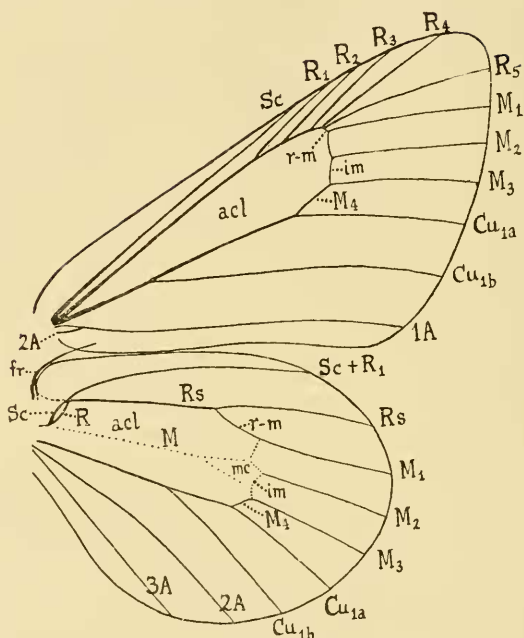
(1) In the forewing, R_{2+3} and R_{4+5} come off widely separated from the main stem of R . This is a characteristic of the pupal forewing of all true Butterflies (with a few exceptions in very highly specialised cases), and marks *Euschemon* definitely as belonging to the Rhopalocera.

(2) Although R_{2+3} is much shorter than R_{4+5} , it forks nearer to the base than does the latter. This agrees with *Xyleutes*, *Wingia*, etc., but differs from the more archaic condition seen in the *Hepialidae*.

(3) In the hindwing, Sc and R_1 fuse to form a single vein; but trachea Sc is dominant, as in *Xyleutes*; whereas, in *Carpocapsa*, *Wingia*, and *Doratifera*, R_1 is dominant.

(4) The development of a very broad humeral area in the hindwing has thrown the frenulum back right to the extreme base of the wing (Text-fig. 100), carrying with it the remnant of the humeral veinlet, which appears as a pale band in the early pupa, but does not become fully chitinised in the imago. Probably correlated with this is the shortening of the separate basal portions of Sc and R_1 in the imago to form a small loop. This loop is characteristic of the *Hesperiidae*; and, in many genera, the veinlet hm is to be seen projecting from it basad. much more strongly than in *Euschemon*. In other Butterflies, this loop is reduced to a minute vestige, or completely closed up.

(5) In the early pupa, M_5 forms as a very distinct pale band



Text-Fig. 100.

Euschemon rafflesia Macleay, (fam. *Hesperiidae*), imaginal venation (x 24). Lettering as on p. 535.

in the usual position, as shown in Text-fig. 99, *b*. Later on, a huge mass of vein-chitin is laid down over the bases of the main veins, and M_5 becomes completely enclosed within it. Trachea M_5 does not appear until near metamorphosis.

(6) The cross-vein *cu-a* is laid down as a pale band in the forewing only, in the early pupa, as shown in Text-fig. 99, *b*. It suffers the same fate as M_5 , being swallowed up in the mass of vein-chitin which forms around it later on.

(7) Tracheae M and Cu_2 remain complete throughout pupal life. But no chitinisation takes place either along Cu_2 or along any part of M lying within the basal cell.

(8) In the forewing, no chitinisation takes place along R_{4+5} , from its origin on R to the point where it forks. This is an important point to bear in mind when studying the method of formation of the basal cell at metamorphosis.

(9) In the forewing, the distal end of 2A lies alongside 1A; the anal Y-vein formed around them is very prominent in the pupal wing, but is reduced to a very small size in the imago.

(10) In the hindwing, trachea 1A appears to have been completely eliminated, as in *Doratifera*. Thus there is no basal Y-vein, and the two anal veins present in the imaginal wing are 2A and 3A, not 1A and 2A as has hitherto been believed. (See Section v.)

At metamorphosis, the changes that take place are much the same as those already described for *Wingia*, except that there is a much greater comparative increase in the size of the wings. The basal part does not increase at all in size; and, consequently, the bases of the tracheæ together with the vein M_5 and the anal loop, become crowded together close to the base, and are hard to make out in the imago. The shape of the forewing alters greatly, the base becoming very narrow, by reduction of the anal area, while the distal margin expands, giving the whole wing a triangular shape. In the imago, only the barest remnant of the anal loop can be seen, while 3A is entirely lost in the forewing. The hindwing broadens out on the whole, but its anal area becomes narrowed, instead of widened as in *Wingia*; 3A is only weakly chitinised.

Tracheæ M and Cu are so close in the wings of this insect at metamorphosis, that the transfer of Cu_1 to M, via M_5 , takes place without any appreciable change in direction; and the serial vein which has M_5 for its basal piece, and Cu_1 as its distal continuation, is practically a straight line. Moreover, although trachea Cu partly shrivels up, as in *Wingia*, it appears to become actually enclosed within the thick chitinisation that forms the base of this serial vein. For, in a carefully prepared cleared forewing of *Euschemon*, taken from a specimen that had emerged only four hours previously, I could plainly see the remains of Cu, with its forking into Cu_1 and Cu_2 , lying just below M_5 within this vein. On the other hand, Cu_2 loses its trachea entirely, and is not chitinised in either fore or hind wing.

The completion of the basal cell at metamorphosis is a process of great interest in this insect. If we look at Text-fig. 99, a, we shall see that the narrow cell bounded posteriorly by R_{4+5} , anteriorly partly by the main stem of R. and partly by R_{2+3} , and closed distally by the short cross-vein *ir* between R_3 and

R_4 , is really the radial cell or areole, which has become sessile upon R , owing to the separation of R_{2+3} and R_{4+5} basally. At metamorphosis, not only all that part of trachea M , lying within the basal cell, becomes aborted, but also the stem of R_{4+5} , which properly separates the areole from the basal cell. Thus, in the imaginal forewing, the basal cell becomes an *areocel*, and is the homologue of the basal cell of the Tortricina and Tineina. The actual method by which this change is brought about is the same as that already seen in *Wingia*, viz., a trachea from R_5 captures M_1 , and another trachea from R_3 captures R_4 and R_5 . Hence all the tracheæ from R_4 to M_1 become hitched on to R_3 , so that trachea R appears, at metamorphosis, as a trachea having six branches all given off anteriorly in order. M_3 is captured by Cu_{1a} , as in *Wingia*. But M_2 loses its tracheal supply, and fails to become annexed by either the radial or cubital group of tracheæ.

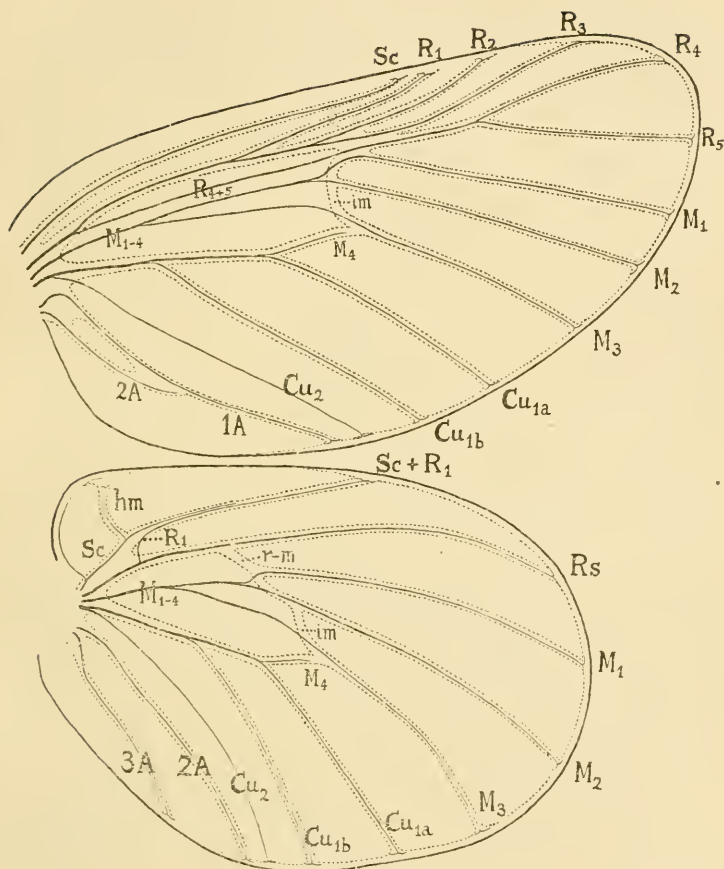
In the hindwing, M_1 is captured by Rs at metamorphosis, and M_3 by Cu_{1a} . But, as in the forewing, M_2 loses its tracheal supply, and fails to become annexed to either group. Though the vein M_2 is chitinised in *Euschemon*, it tends to become aborted in many *Hesperiidae*, and its loss is primarily due to the failure to secure a tracheal supply.

Text-fig. 100 shows the imaginal venation of *Euschemon*, for comparison with Text-fig. 99.

As a contrast to *Euschemon* I studied the pupal tracheation of one of the highly specialised *Nymphalidae*, *Euploea corinna*. Text-fig. 101 shows the condition of the wings in a pupa of this species about three days old, the veins and tracheæ being indicated in the same manner as in Text-fig. 99. The only important differences are as follows:—

(1) In the forewing, I could find no sign of M_5 ; and M_{1-4} forks much closer to the base of the wing than in *Euschemon*. Also $2A$ is greatly reduced, and $3A$ completely absent. Besides these differences, there is a fairly strong tracheal outgrowth from Cu_{1a} along the vein M_4 towards M_3 . This is the same outgrowth which appears in *Euschemon* at metamorphosis. The condition in *Euploea* is, then, an advance upon that seen in *Euschemon*.

(2) In the hindwing, the condition of M is as in the forewing. R_1 comes off from the main stem of R in a highly specialised manner, but is dominant over Sc . The latter trachea gives off a

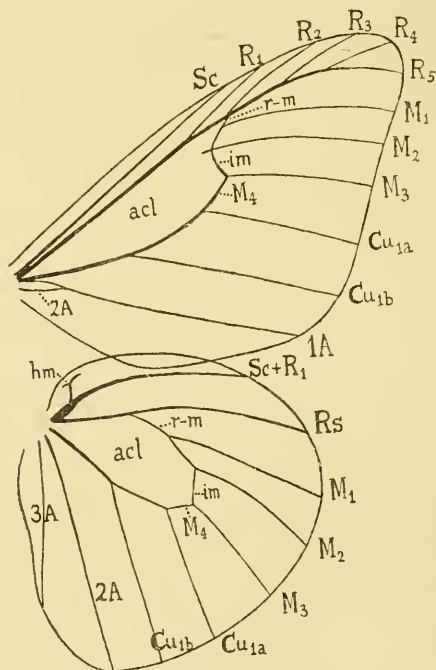


Text-Fig. 101.

Euploea corinna Macleay, (fam. *Nymphalidae*), tracheation of wings of three-days-old pupa, (x 4). The pale bands foreshadowing the imaginal venation are shown by the double dotted lines. Lettering as on p. 535.

definite branch to *hm* (this does not occur in *Euschemon*, and there is also a second branch arising from the extreme base of *Sc*, and running to where the frenulum would be situated if it were present. The trachea outgrowing from *Cu*_{1a} along *M*₄ is smaller than in the forewing. 2A and 3A are present, but 1A and the basal Y are absent, as in *Euschemon*.

The changes at metamorphosis are the same as in *Euschemon*, resulting in the formation of an areocel in the forewing, and a generally similar type of venation. The chief differences lie in the retention of a short spur of M_{1+2} within the basal cell of the forewing, and in the anal Y-vein remaining quite as large as it was in the pupal wing (Text-fig. 102), and hence somewhat more conspicuous than in the imago of *Euschemon*. In some *Nymphalidae*, not only a short spur of M_{1+2} , but also corre-



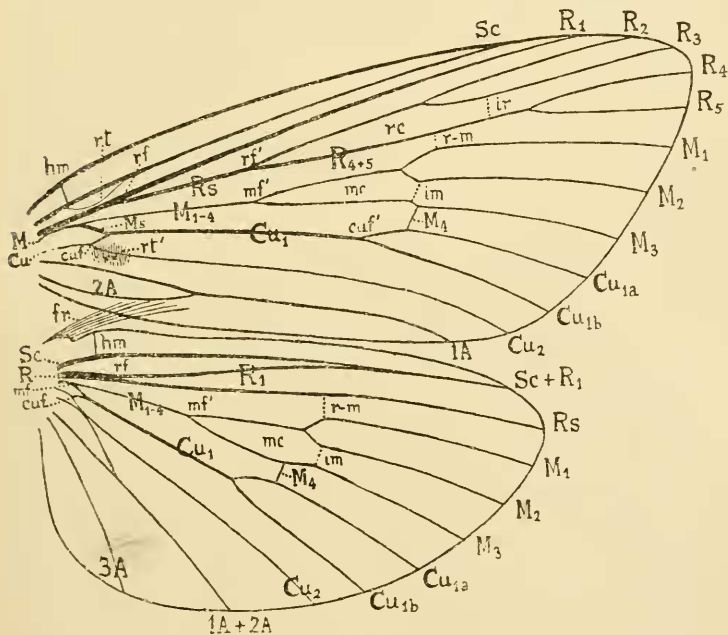
Text-Fig. 102.

Euploea corinna Macleay, (fam. *Nymphalidae*), imaginal venation, (x $1\frac{1}{2}$). Lettering as on p. 535.

sponding spurs of R_{4+5} and M_{3+4} , may be seen projecting into the cell of the forewing; while, in the hind, the positions of the same structures may be indicated by knobs or swellings. These are easily to be seen in the large *Danainae*, e.g. *Danaida archippus* Fabr. In the hindwing, the small closed space between Sc

and R_1 basally is obliterated in *Euploca*, though a remnant of it may still be seen in *Danaidia*. The veinlet *hm* develops into a strong costal spur, which helps to strengthen the enlarged amplexiform humeral area. Text-fig. 102 shows the imaginal venation of *Euploca corinna*, for comparison with that of *Euschemon rafflesia*.

The Archetype of the Suborder Heteroneura may now be determined, by summing up the characters of the various groups studied, and selecting the most archaic condition of each. This is most conveniently done by means of a Table (Table iv.) similar to that already given for the Homoneura, in which the letter A indicates the most archaic condition for each character, while B, C, . . . indicate more specialised conditions in ascending order. The Rhopalocera are included in this Table, though not strictly one of the more archaic groups of this Sub-



Text-Fig.103.

Wings of the Archetype of the Suborder Heteroneura. Lettering as
on p.535.

order, because they have been studied in this Section, and a tabulation of their characters for comparison with the older groups may prove of great value later on in helping to solve the problem of their origin. On the other hand, the fossil *Palaeontinidae* have been omitted; for, as already indicated, there is no proof that they have been derived from the old Homoneurous stem of the Order along the same line of descent as our present-day Heteroneura. They are best treated as an entirely separate group, until, perhaps, further discoveries, or more detailed study of the existing fossil types, may have demonstrated conclusively where they properly belong.

Text-fig. 103 gives a diagrammatic representation of the wing-venation of the Archetype of the Heteroneura. The Table shows conclusively that, of all existing Heteroneura, the *Cossidae* stand far nearer to this Archetype than do any other group. Thus Dr. Turner's name of *Protocossidae* for the archetypic family of the Suborder is fully justified. Next to the *Cossidae* would come the most archaic Tineina, such as *Titanomis*, and then the *Castniidae* and the bulk of the Tortricina and Tineina. The groups above these are more highly specialised.

It is interesting to compare the Archetype of the Heteroneura with that of the Homoneura, i.e. of the whole Order Lepidoptera. The characters in which it is specialised may be briefly stated as follows:—

- (1) Absence of the distal forking of Sc.
- (2) Absence of the distal forking of R_1 .
- (3) In forewing, R_{2+3} forks nearer to base than does R_{4+5} .
- (4) In hindwing, Sc and R_1 are fused distally.
- (5) In hindwing, R_s is a simple, unbranched vein.
- (6) M_4 is already placed in a transverse position, resembling a cross-vein, and its trachea is, at the most, only feebly developed.
- (7) The cubito-median Y-vein, though present, is never so typically developed as in the Jugo-frenata.
- (8) 3A is absent from the forewing, though present in the hind.
- (9) Only a single Y-vein is present in the anal area of the forewing.
- (10) 1A and 2A are fused near the base in the hindwing, to form an anal Y-vein.
- (11) The following cross-veins are absent:—*sc-r*, *cu-a*, *ia_1*, *ia_2*, and *sa*.
- (12) The shape of the wings is much altered from the ori-

ginal, the forewing already having the apex well forward and a distinct termen, while the hindwing has its costal, subcostal and radial areas much narrowed (and consequently their venation much reduced), but its anal area widened.

In connection with characters (1), (2), (7), (8) and (12), together with the retention of the cross-veins *ir*, *r-m* and *im*, and the increase in size of the anal area and its veins, note the close parallelism between *Stenopsychodes* and its allies in the Trichoptera (p. 629), and that of the Archetype of the Heteroneura in the Lepidoptera. If the family *Polycentropidae* had continued this line of evolution, by reducing the subcosta and radius of the hindwing, there would have resulted a group of Caddis-flies closely comparable with the Heteroneura amongst the Lepidoptera.

The "percentage archaism" of the Archetype of the Heteroneura, as compared with that of the Order, if worked out on the twenty characters given in Table iii. on p. 650, will be found to be 52.5, i.e. less than that of the *Micropterygidae*, *Eriocraniidae* and *Hepialidae*, as might have been expected. But a fairer comparison would be obtained by adding to this Table also those characters given in Table iv. on p. 690 in which the Heteroneura are specialised, but which are not included in Table iii., since they do not come into question in the case of the Homoneura. By this method, a percentage archaism of 44.4, out of a total of twenty-seven characters, will be obtained; and this percentage, I think, very fairly represents the correct position of the Archetype of the Heteroneura in the evolution of the Order.

By multiplying the percentages obtained in Table iv. by the factor 0.444, we can obtain a comparison of the "percentage archaisms" of the various groups of Heteroneura, when the percentage for the Archetype of the Order, and hence of the Homoneura also, is given as 100. To make this comparison fair for the Homoneura also, we must add to the twenty characters given in Table iii. the seven characters in which the Archetype of the Heteroneura is specialised, and in which, therefore, *all* the Homoneura must be credited with an extra seven "A's" The combined results will then be as follows:—

Micropterygidae 79.5, *Eriocraniidae* 72.2, *Hepialidae* 70.3, *Prototheoridae* 53.7, *Cossidae* 41.7, *Mnesarchaeidae* 38.9, *Tineina* 33.3, *Castniidae* 30.7, *Tortricina* 27.8, *Psychina* 22.2, *Pyralidina* 18.2 and *Rhopalocera* 15.3.

TABLE IV.

PRINCIPAL VENATIONAL CHARACTERS FOR THE MORE ARCHAIC GROUPS OF THE HETERONEURA, AND FOR THE BUTTERFLIES, BUT EXCLUDING THE FOSSIL PALÆONTOIDEA.

| Ref. No. | Character. | Cossidae. | Tortricina. | Tineina. | Castniidae. | Psychina. | Pyralidina. | Rhopalocera. |
|---|--|-----------|-------------|-----------|-------------|-----------|-------------|--------------|
| (1) | Sc and R ₁ in pupal hindwing:—A. Fused for distal half only. B. Fused more than half their length. | A. | A. | A or B. | ? | A. | ? B. | B. |
| (2) | Condition of Rs in pupal forewing:—A. A single sector, branching dichotomously, with fork of R ₂₊₃ nearer to base than that of R ₄₊₅ . B. Single sector, with R ₃ transferred to R ₄₊₅ . C. R ₂₊₃ and R ₄₊₅ arising separately from R. | A. | A. | A. | A. | B. | ? B or C. | C. |
| (3) | Rs in pupal hind wing:—A. Reduced to a simple, unbranched vein. B. Ditto, with capture of trachea M ₁ . | A. | A. | A. | ? | B. | ? B. | A. |
| (4) | Condition of radial cell or areole in pupal forewing:—A. Present, closed by cross-vein <i>ir</i> . B. Present, closed by fusion of R ₃ with R ₄₊₅ (<i>ir</i> absent). C. Absent. (*areole sessile on main stem of R). | A or B. | A. | A. | A or C. | C. | ? | A.* |
| (5) | Basal cell and areole in imaginal forewing:—A. Separate. B. Forming a single areocel. | A. | A or B. | A or B. | A. | A. | ? | B. |
| (6) | Condition of M ₁₋₄ within basal cell of forewing:—A. Fully present. B. Incomplete. C. Absent. | A. | B or C. | A, B or C | A or B. | A or B. | C. | C. |
| (7) | Condition of M ₅ in imaginal forewing:—A. Distinct. B. Reduced or aligned with Cu _{1a} . | A. | B. | B. | B. | B. | B. | B. |
| (8) | Trachea M ₁ in pupal wings:—A. Small, present. B. Absent. | A or B. | B. | B. | B. | B. | B. | B. |
| (9) | Condition of vein Cu ₂ in imaginal wing:—A. Present in both wings. B. Present in hind, but reduced, weak or absent in fore. C. Absent, or nearly, in hind, weakened in fore. D. Absent in both. | A. | B. | B. | C. | A. | B. | D. |
| (10) | Basal fusion of tracheæ Cu ₂ and 1A in pupal hindwing:—A. Completed. B. Nearly complete. C. Absent. | B. | B. | A. | ? | C. | C. | C. |
| (11) | Anal Y-vein of forewing:—A. Present. B. Very small. C. Incomplete. D. Absent. | A. | A. | A-D | A or D. | A. | C or D. | B or D. |
| (12) | Condition of 1A and 2A in hindwing:—A. Fused to form a small basal Y-vein. B. Reduced to a single vein. | A. | A. | A or B. | A. | B. | A or B. | B. |
| (13) | 3A in hindwing:—A. Present. | A. | A. | A. | A. | A. | A. | A. |
| (14) | Humeral veinlet:—A. Present in both wings. B. Present in one wing only. C. Absent from both wings. | A or B. | C. | C. | C. | C. | C. | B. |
| (15) | Cross-vein <i>im</i> :—A. Present. | A. | A. | A. | A. | A. | A. | A. |
| (16) | Cross-vein <i>r-m</i> :—A. Present. | A. | A. | A. | A. | A. | A. | A. |
| Percentage of archetypic characters present in most archaic representatives of each group (excluding undetermined characters):— | | 93·8 | 62·5 | 75·0 | 69·2 | 50·0 | 40·9 | 34·4 |

Note:—The percentages given for the *Castniidae* and *Pyralidina* in the above Table cannot be accurately determined until the tracheation of the pupal wing can be examined. If all the doubtful characters in the case of the *Pyralidina* were thus to be proved to be archaic (a very unlikely happening), the percentage for this group would be raised to 59·4; whereas, if they were all to be proved to be specialised, the percentage would be lowered to 28·1.

Section xv. THE VENATION OF THE MEGALOPTERA.

(Text-figs. 36*a*, 39-40, 44, 47*a*, 104-108.)

This Order, as at present constituted, consists of a small number of archaic types not very closely related amongst themselves. Probably none of their ancestors has ever been dominant at any time, and this may well be the reason why, though the Order contains chiefly forms with aquatic larvæ and inhabiting the banks of streams, the fossil record is exceedingly poor.

Some authors, including Handlirsch (2), consider the terrestrial Raphidioidea to belong to a separate Order, distinct from the Sialoidea. Others again merge the Megaloptera with the Planipennia into a single Order Neuroptera. I have, for the present, taken the intermediate course of uniting the two groups Raphidioidea and Sialoidea into a single Order Megaloptera, while keeping the Planipennia distinct. The important point is not whether there are one, two or three Orders represented, but rather that we should keep clearly in mind the different lines of evolution indicated, whether we choose to class them as belonging to one, two or three Orders. It will be seen in the sequel that differences of opinion on this latter point will not appreciably affect the definitions of the Archetypes involved; and, as far as the venational scheme is concerned, at any rate, the evidence will be found to favour only one conclusion.

The problem of determining the Archetype of the Megaloptera is not an easy one. In order to grasp the problem fully, it will be necessary to figure examples of all the different types known in the Order. This I have done in Text-figs. 104-107.

There are two Sub-orders, viz. the Sialoidea, consisting of forms whose larvæ are aquatic or semi-aquatic, and the Raphidioidea, whose larvæ are terrestrial. The latter are, in most respects, rather highly specialised insects. But they cannot be descended directly from the Sialoidea, because they all possess the original condition of having Sc and R₁ quite separate in both wings; whereas all the known Sialoidea have these veins fused distally, as in the higher Planipennia. We may, for the present, dismiss the specialisations shown by the Raphidioidea from our minds, and only remember that this condition of a separate Sc and R₁ has to be present in any Archetype from which they can possibly have been derived.

The Sialoidea are universally admitted to be more archaic than the Raphidioidea. It is also generally agreed that the family *Corydalidae* (Text-figs. 105, 106) is more archaic than the family *Sialidae* (Text-fig. 104), these being the only two families represented within the Suborder. It is in the comparison of the venational types found in these two families that we meet with our principal difficulties in the construction of the Archetype of the Order.

The outstanding feature of the venation of the two Neuropteroid Orders, Megaloptera and Planipennia, as contrasted with that of the Panorpoidea, is the generally strongly developed tendency towards the pectination of Rs. This character is beautifully illustrated in almost all Planipennia, but is by no means so evident in the older Megaloptera. We have here to study this peculiarity, and to decide what the archetypic condition was, from which the pectinate type of Rs was originally evolved.

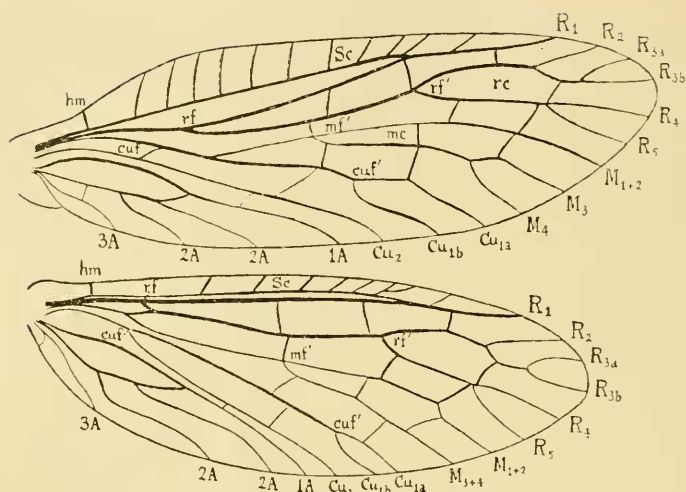
A little consideration will show us that the tendency towards pectination in Rs probably did not, at first, affect R_{4+5} ,* but only R_{2+3} . For, in all the *Sialidae*, R_{4+5} remains still dichotomously branched, as shown in Text-figs. 47a, 104; while, in the *Corydalidae*, where the pectinate form of branching of Rs is generally much more in evidence, there are many examples of the retention of the original dichotomic forking of R_{4+5} , as, for instance, in *Protohermes* (Text-fig. 106). Further, in those genera in which pectination has become more complete, through the loss of the original fork of R_{4+5} (as in *Archichauliodes*, Text-fig. 105, *Chauliodes*, *Corydalus* and allies), specimens are not infrequently found with this fork retained in one or more wings. Thus we must conclude that, in the Archetype of this Order, pectination of Rs, if present, had only affected R_{2+3} .

Our next difficulty lies in the presence of some forms in which no pectination of Rs is visible at all, and from which we might be led to the conclusion that the Archetype of the Order had a dichotomic Rs. I refer in particular to the Australian genera *Austrosialis* and *Stenosialis*, which are reduced archaic offshoots from the family *Sialidae*. In Text-fig. 47, I compared the venation of *Austrosialis* with that of the Trichopteron *Rhyacophila*,

*See, however, footnote on p.552, and Text-fig.39. The vein taken to be R_{4+5} may possibly have been an originally branched R_5 .

and showed how remarkable it was that these two genera should possess exactly the same type of branching of all the veins, in both fore and hind wings. At first sight, one is tempted to postulate a Megalopterous origin for the Trichoptera, and to say that *Rhyacophila*, and therefore the Order Trichoptera, must have originated from a type very close to *Austrosialis*. But a little consideration will show us that this would be a very serious misinterpretation of the actual facts of the case. The *Sialidae* are the most highly specialised of the aquatic Megaloptera, and are undoubtedly derived from ancestors that were more like the *Corydalidae*. *Austrosialis* is much more highly specialised than *Rhyacophila* in the very long and complete fusion between Cu_1 and M_{1-4} ; the consequent loss of all traces of the cubito-median Y-vein; the removal distad of the secondary radial fork, and consequent reduction in the length of the branches of R_s ; and the distal fusion of Sc with R_1 . *Rhyacophila*, on the other hand, is specialised in quite a different direction, in having the anal veins of the forewing completely looped up into a double Y-vein. There are, of course, many other differences, but those mentioned will suffice for our purposes. Complete proof or disproof of any suggested origin of the Trichoptera from the *Sialidae* could only be supplied by a study of many other characters besides the venation; and the possibility of such a descent will again be discussed in the part of this research which has to deal with larval characters. For the present, we must put it aside, and see only in the resemblances between *Austrosialis* and *Rhyacophila* a very striking instance of parallel development, between two widely separated types which, as we shall see later on, have nevertheless had a common origin in a more remote period.

If we compare *Austrosialis* (Text-fig. 47a) with *Sialis* (Text-fig. 104), we can see in the latter the preservation of the old Corydalid tendency to pectination of R_{2+3} . For, by comparing the radial sector of this latter genus with that of *Archichauliodes*, we see at once that suppression of the original terminal forking of R_2 , with a shifting of the tips of R_{2+3} somewhat costalwards along the wing-margin, would result at once in the form found in *Sialis*. Moreover, the extra branch of R_2 is also frequently present in specimens of the genus *Sialis* (though not in the example figured), but is usually found to have migrated across to the base of R_3 ; so that the type of pectination found in this



Text-Fig. 104.

Wings of *Sialis lutaria* Linn., (fam. *Sialidae*), (x 6). Lettering as on p. 535.

genus tends to become unique in having the terminal branches of R_{2+3} arranged anteriorly, instead of posteriorly.

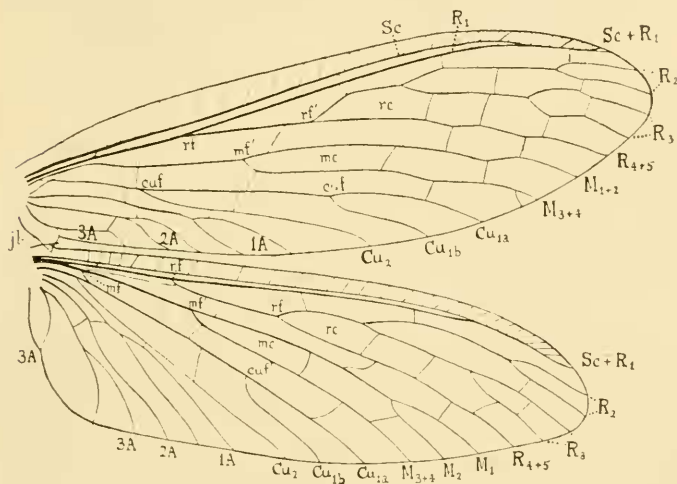
It should be noted here that there is really no justification for the assumption that there has been any constant addition to the branches of the main veins in the *Sialidae*, by terminal twigging or splitting, such as is found in the Planipennia. No such additions are to be found either upon M or Cu; and it is purely a gratuitous assumption to say that they are present on Rs, when the condition of that vein is much more reasonably derived directly from the older Corydalid type.

We may, then, fairly assume that the *Sialidae* are a reduced offshoot from the older *Corydalidae*. Such a conclusion is supported by the whole weight of the evidence from other characters, the *Corydalidae* being, both in their morphology and life-histories, by far the more archaic of the two families.

A typical archaic Corydalid genus is the Australian *Archichauliodes* (Text-fig. 105). In this genus, Cu retains the original three-branched condition, without any alteration in the position of its forkings; M is generally reduced either to three

or two branches; and R_s retains the terminal dichotomic forkings of R_2 and R_3 , though generally (but not always) the original dichotomy of R_{4+5} is suppressed.

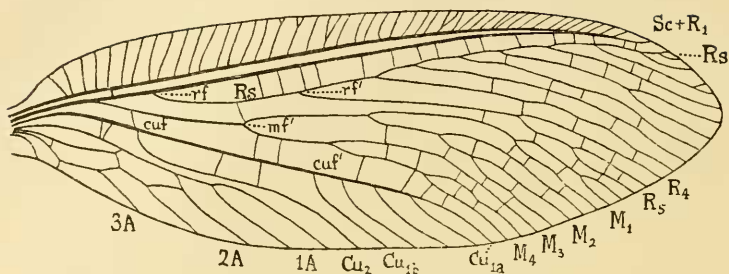
We must now contrast this with the somewhat different type shown in *Protohermes* (Text-fig. 106), claimed by van der Weele to be the most archaic type within the Order.



Text-Fig. 105.

Wings of *Archichauliodes guttiferus* (Walk.), (fam. *Corydalidae*), (x 2.7). Lettering as on p. 535.

The first thing to be noted in *Protohermes* is the clear evidence of *addition* of extra branches to the main veins, on the Plannipennian plan, from the tip inwards. This is best seen in the case of Cu_1 , which has become transformed from its original dichotomic condition into a pectinate vein, on the lines indicated in Text-fig. 40. The same thing has happened with M , although it seems also quite clear that this vein possessed at least four branches when the additions began, seeing that both M_{1+2} and M_{3+4} fork dichotomically at about the same level as the original forking of Cu_1 . Some of the branches of R_s have evidently been added from the tip backwards also; but there is certainly no evidence to restrict the original number of branches of this vein to four.



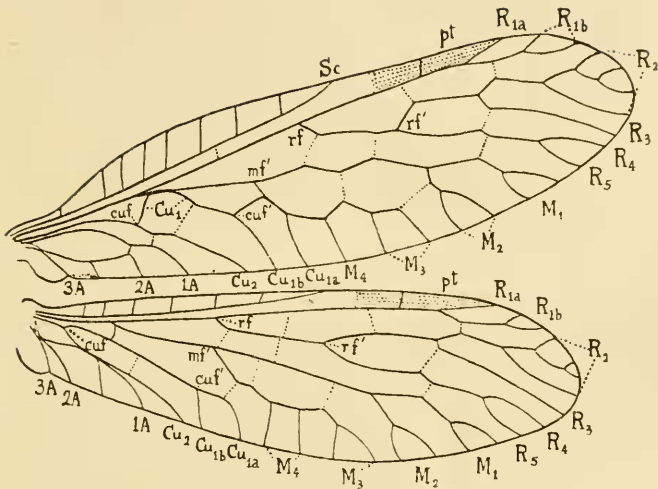
Text-Fig. 106.

Forewing of *Protohermes davidi* Weele, (fam. *Corydalidae*), (from van de Weele, but with lettering added, as on p.535).

A fair judgment between the two types shown in *Archichauliodes* and *Protohermes* would, I think, refuse to recognise that one type was at all more predominantly archaic than the other. Both are derivable from a very close common ancestor, in which, on the one hand, no reduction had occurred in the number of branches of M, and, on the other, no additions had been made to the venation from the tips of the veins inwards. Such a type would have to possess the following venational characters:—At least six branches of Rs, viz. a dichotomic fork of R₂, a similar one belonging to R₃, and the original fork of R₄₊₅ still preserved; four branches of M₁₋₄, arranged in the original dichotomic manner; and a normal, archaic, three-branched Cu.

This common type will be seen at once to be the Archetype, not only of the family *Corydalidae*, but also of the family *Sialidae*, and hence of the whole Suborder Sialoidea. We have now to consider what modifications are required in it, in order that it may also be the Archetype of the Raphidioidea, and therefore of the whole Order.

Text-fig. 107 shows the venation of *Raphidia maculicollis* Steph. The specialisations to be seen in this type are chiefly those by which the original courses of the main veins and their branches have been greatly altered from the normal condition. M has become strongly fused basally with R; and, in the forewing, Cu₁ has become very strongly fused with M. The terminal twiggings of R_{1b} and the upper branch of R₂ are clearly



Text-Fig. 107.

Wings of *Raphidia maculicollis* Steph., (fam. *Raphidiidae*). ($\times 7\frac{1}{2}$).

• Lettering as on p. 535. The cross-veins are indicated by dotted lines.

additions to the original venational scheme; and it is probable that the same cause has operated to produce the extra forks of M. As against these specialisations, we find Sc and R_1 remaining unfused distally, and no sign of any tendency towards expansion of the anal area of the hindwing, such as is very obvious in all the Sialoidea.

We should also note that, in the Sialoidea, there is no fusion of 1A with Cu_2 in the hindwing, though the two veins approach very close to one another. This fusion is completed in the Raphidioidea, as already mentioned in Section v.

As regards the costal veinlets, there is a complete system present in all Megaloptera, and hence also in the Archetype.

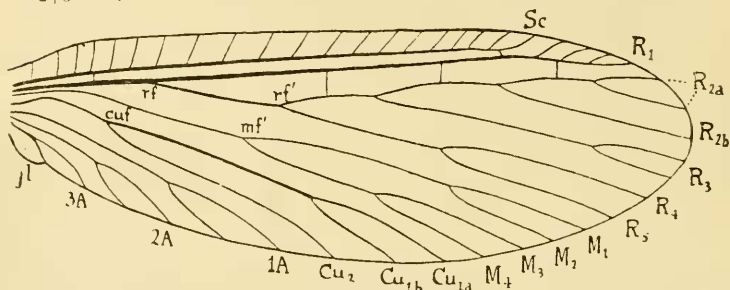
The cross-vein system can be seen to be closely similar in *Raphidia*, the *Sialidae* and *Archichauliodes*, but is most primitive in the last-named, where there is little tendency to any definite arrangement. A constant character is the presence of only *three* cross-veins between R_1 and R_5 . The addition of numerous cross-veins between these two main veins in *Protohermes* (Text-fig. 106) is clearly not an archaic character, as

van der Weele imagined, but is correlated with the increase in the number of pectinate branches of Rs.

We are now able to construct our Archetype, of which we have figured the forewing only, in Text-fig. 108. The characters which mark this type may be briefly stated as follows:—

(1) Sc and R_1 distinct, not fused distally, and a complete series of costal veinlets present.

(2) Rs with more than four original branches, and with a tendency towards a pectinate arrangement of these branches in R_{2+3} only.



Text-Fig. 108.

Forewing of the Archetype of the Order Megaloptera. Cross-veins omitted, except only those between Sc and R_1 and between R_1 and Rs, which are constant. Lettering as on p.535.

(3) Cubito-median Y-vein reduced, with M_5 weakly formed and failing to make a strong union with Cu_1 in forewing; in hindwing, this Y-vein is fairly normal.

(4) M_{1-4} with only four branches, dichotomically arranged.

(5) Cu three-branched, Cu_1 being distally forked, as in *Paramecoptera*, *Trichoptera* and *Lepidoptera*.

(6) No fusion of 1A with Cu_2 in hindwing, but these two veins approach close to one another in both wings.

(7) Cross-vein system rather irregular, widely spaced, not very numerous; only three cross-veins between R_1 and Rs.

In constructing the above Archetype, I have not brought into consideration the two known Lower Triassic fossil genera which are supposed to belong to this Order. These are *Chauliodites* Heer and *Triadosialis* Heer. The former does not seem to me to be definitely Megalopterous; the latter is very probably a somewhat reduced Corydalid type, and falls well within the

archetype definition. It has a pectinate Rs, and both M and Cu are three-branched.

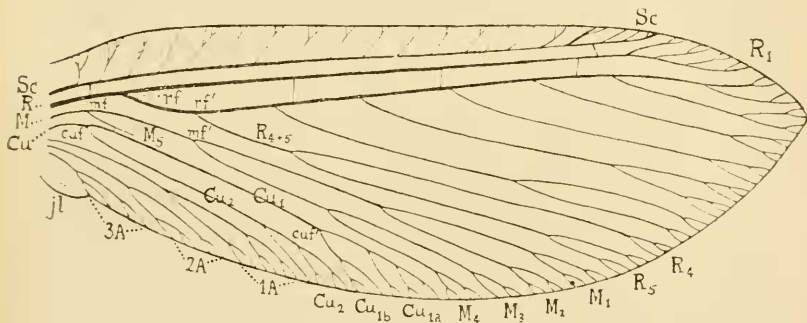
It will be realised, from Text-fig. 108, that the Archetype of the Megaloptera possesses a very primitive type of venation; and that it is older, in some respects, than the Permian *Belmontia*. This speaks for a very ancient origin for the Order. The question is more fully discussed in Section xvii.

Section xvi. THE VENATION OF THE PLANIPENNIA.

(Text-figs. 36a, 39-40, 45, 52, 109-110.)

This Order is the dominant one amongst the Neuropteroidea, and exhibits a wealth of venational specialisations not equalled in any other known Order, except perhaps in the Odonata. To deal with all these would take us far beyond the limits set down in this Part. I shall confine myself here strictly to the construction of the Archetype of the Order, while leaving a fuller discussion of the internal phylogeny of the different families for a later paper. In this connection, it is only necessary to refer the reader to the excellent figures and descriptions given by Comstock (15, chap. ix.), which will be mentioned also when certain types are being discussed.

The fossil record of the Planipennia, unlike that of the Mega-



Text-Fig. 109.

Forewing of an archaic representative of the family *Prohemerobiidae*, with R_{4+5} still dichotomously branched. The same type will stand for the Archetype of the Order Planipennia. Cross-veins omitted, except only those between Sc and R_1 , and between R_1 and R_2 , which are constant. Lettering as on p.535.

loptera, is a rich one. It begins in the Upper Triassic of Ipswich, Queensland, and continues through the Lias and Upper Jurassic of Europe. The dominant type of Planipennian wing present in all these strata is that belonging to the family *Prohemerobiidae* (Text-fig. 109). This may be defined as a very primitive type, having no distal fusion of Sc with R_1 , no specialisation of the main stems of Sc, R_1 and Rs to form a *vena triplica* like that of the *Psychopsidae*, and no definitely arranged system of cross-veins. Superimposed upon this very archaic foundation is a highly specialised condition of the radial sector, in which the pectinate condition of the branches is very clearly marked.

The oldest known fossil Planipennia, viz. *Archepsychops* (28) and *Protopsychoptis* (5) of the Ipswich Trias, are definitely Prohemerobiid types, as I have already proved. The former, moreover, shows such close affinity with the still existing *Megapsychops* of the family *Psychopsidae*, that there can be no doubt of the origin of this latter family as a direct offshoot of the ancient Prohemerobiid stem (28).

We have now to consider whether there may not still exist some archaic type, which may be considered to be either truly Prohemerobiid in itself, or even, perhaps, older than the fossil types so far discovered. Such a type is surely to be found in the *Ithonidae* (12, 30), an archaic side-branch of the Order, confined to Australia, and differing from all the other Planipennia in the possession of a melolonthoid larval type, in which the paired sucking jaws are of a very primitive form.

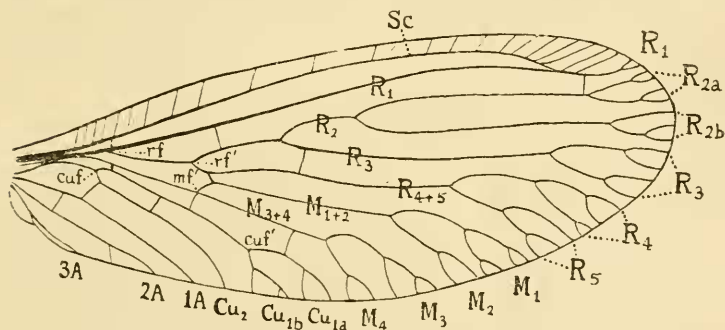
The type of venation in this family is definitely Prohemerobiid, but even more archaic than are many of the fossils of that family, in that the dichotomic forking of R_{4+5} * is still preserved in the majority of specimens; and the resemblance to the Megalopterous type of venation is even closer than is the case with the fossils.

The specialisations to be seen in the venation of *Ithone*, apart from the pectination of Rs already mentioned, are the abundant additions to the branches of the main veins, in the form of terminal twigs or branchlets, and the apparent complete loss of M_5 . The former is an ordinal character for the Planipennia, being clearly shown in all types except the excessively reduced

*See foot-notes on pp. 552, 692.

Coniopterygidae, which may well have been descended from forms which originally possessed it. The loss of M is also to be noted in most families of the Order; but this vein has been found by me in the fossil *Archepsychops*, as well as in recent *Psychopsidae* (Section iii.).

Another archaic existing family is the *Sisyridae* (Text-fig. 110), in which clear evidences of reduction from the Prohemerobiid type may still be found; though the specialisation of the larva for feeding upon fresh-water sponge, and the heavy re-



Text-Fig. 110.

Forewing of *Sisyra brunnea* Banks, (fam. *Sisyridae*), (x 17). Lettering as on p. 535.

duction in size, and consequently in density of venation, undergone by the imago, have considerably simplified the general scheme. The pectination of R_{2+3} is as clearly evident as is the retention of the original dichotomy of R_{4+5} . Further, the condition of M, when compared with that of Cu, shows the strong probability of the former having been originally four-branched, though most families of the Planipennia have this vein only two-branched. It will be clear that, quite apart from the smaller terminal twigs of normal Planipennian type, the series of forks marked x , y , z , and cuf' are certainly homotypic, and must therefore either all represent additions, or all be part of the original archaic venational scheme. Now the condition of Cu, apart from the terminal twigs, is quite primitive, and shows the three-branched condition quite clearly, as in the Megaloptera, Trichoptera and Lepidoptera. The point marked cuf' is clearly the secondary enbital fork, at which Cu_1 divides into

Cu_{1a} and Cu_{1b}. Likewise also the fork marked *x* clearly represents the archaic position of the fork of R₄₊₅; while it is even possible that the vein above it, R₃, may also have preserved a somewhat smaller fork. Thus we can only conclude also that the forks *y* and *z*, belonging to M₁₊₂ and M₃₊₄ respectively, are the original forkings of those veins, and not additions like the smaller terminal twigs.

Closely allied to the *Sisyridae*, but less reduced, are the terrestrial *Berothidae* (in which the *Trichomatidae* may be also included as, at most, a distinct subfamily). They are, however, specialised by the long series of pectinate descending branches of Cu₁ in the hindwing. The affinity of this family with the *Prohemerobiidae* is quite obvious.

The *Hemerobiidae* are also a direct offshoot of the *Prohemerobiidae*, specialised by partial fusion of the main stem of Rs with R₁ in the forewing; the result being that some of the pectinate branches of this vein appear to come off from R as separate sectors. *Drepanepteryx* and allies are the most archaic types of this family (12). From these, all stages of reduction to very small, highly specialised forms with reduced venation can be easily followed out.

All the other families of the Planipennia are specialised in one or more directions, and need not be considered here in the construction of the Archetype.

It is an interesting fact that, in the families *Sisyridae*, *Berothidae* and *Hemerobiidae*, in which the cross-vein system is not greatly developed, the same three cross-veins can generally be seen between R₁ and Rs as in the majority of the Megaloptera. Sometimes they are reduced to two in number, as in Text-fig. 110. If, now, we turn to the *Polystoechotidae* (15, fig. 181) we find that, though the number of branches of Rs has greatly increased, the number of cross-veins is still only three or four in this position. It seems fair to conclude from this that the number of cross-veins between these two veins was *originally three* in both Orders, and that the increase seen in *Protohermes* and allied genera (Text-fig. 106) in the Megaloptera, and in the great majority of families of the Planipennia, is correlated with the increase in cross-veins in other parts of the wing.

As all the other families of this Order are specialised in one or more directions, I have omitted them from consideration in the construction of the Archetype. The conclusion we are

bound to come to is that this Archetype was essentially of a Prohemerobiid type, but with R_{4+5} still dichotomically branched, as in Text-fig. 109, which may be taken as the forewing of the Archetype as well as that of a typical Prohemerobiid wing. M_{1-4} was four-branched, and Cu three-branched. Terminal splitting or twigging of the veins is typical of the Order; and this character is therefore included in the Archetype. The system of costal veinlets also tended to split at the tips. The cross-vein system was probably very primitive, but showed a slight specialisation, as in the Megaloptera, in having only three cross-veins between R_1 and Rs , and probably also only two (*sh* and *sc-r*) between Sc and R_1 .

It will now be clear that there is only a single character in the wing-venation of the Megaloptera which is more highly specialised than the corresponding one in the Archetype of the Planipennia, viz., the absence of any remnant of M_5 in the forewings of the former. Apart from this, the Planipennia can be directly derived from the Archetype of the Megaloptera by further increase in the tendency to pectination and addition of branches to Rs , and by the beginnings of the terminal splittings of the veins. Thus the two Orders, in respect of their wing-venation, are barely distinct, and may be shown as a dichotomy from a common stem, which must itself have been derived from somewhere along the original main stem of the Complex, probably somewhat before the point indicated by *Belmontia* in Text-fig. 112. The two Orders are more closely related than are the Trichoptera and Lepidoptera; and those who prefer to merge them into a single whole, as two Suborders of a single Order Neuroptera, are quite logical in doing so. We shall continue to keep them distinct, for purposes of discussion, throughout this research, and shall only make a final decision on the question, when the whole of the evidence bearing upon it has been dealt with.

Section xvii. PHYLOGENETIC RESULTS.

(Text-figs. 38, 111, 112.)

We may now summarise the results of the preceding Sections as briefly as possible, with a view to deducing some phylogenetic conclusions therefrom. We shall arrange these as follows:—

- (1) Construction of the Venation of the Archetype of the Complex.

M_5 forming the upper arm, Cu_1 the lower, and the stem of the Y being the fused vein M_5+Cu_1 , which forks again distally. *Cubitus* three-branched, Cu_1 forking distally after fusion with M_5 , Cu_2 remaining weakly formed and simple. *Anal veins* three in number, all separate, either forked or simple. *Convex veins* R, M_5+Cu_1 and the three anals. *Concave veins* Sc, M_{1-4} and Cu_2 . *Cross-vein system* consisting of very weakly formed cross-veins, more or less irregularly placed, and not in any special positions of mechanical advantage.

Wing-coupling apparatus (24) complete, the forewing with jugal lobe and bristles, the hind with humeral lobe and frenulum.

Wing-trichiation (25) showing both microtrichia and macrotrichia, the former all over the membrane on both sides, the latter confined to the main veins and their branches, including the costal veinlets, and to the archedietyon, which is more or less aphantoneuric.

Fore and hind wings closely similar in shape and venation, but the latter somewhat shorter than the former, more weakly chitinated, and with somewhat shorter Sc.

In repose, the wings are held roof-wise over the back of the insect (*stegopterous* position).

Table of the Characters of the Wings for the Archetypes of the Complex and its Orders. (Table v.)

In the Table here given, the characters of the wings for the various Archetypes constructed in Sections viii.-xvi., and for the Archetype of the whole Complex, are arranged together for comparison. For each character selected, the most archaic condition is indicated by the letter A. This is usually only contrasted with a single specialised condition, represented by the letter B. In the case of characters in which a series of evolutionary stages can be recognised, these are represented by the letters A, B, C. . . ., in ascending order of specialisation.

For the purpose of comparing the venations of the various Archetypes, their respective *Comparative Archaisms* may be calculated. These are defined as "*the percentage of archaic characters retained by the given Archetype.*" The Comparative Archaism for the Archetype of the Complex is, of course, 100, since this type contains all the known archaic features. In calculating the percentages for the other Archetypes, the follow-

ing method has been adopted:—In case of characters represented by A or B only, A scores 1, B nil; for those represented by A, B, C, A scores 1, B $\frac{2}{3}$, C nil; for those represented by A, B, C, D, A scores 1, B $\frac{2}{3}$, C $\frac{1}{3}$, and D nil; and so on. Thus due allowance is made for the possession of any degree of archaism; and the only condition that scores nothing at all is the most highly specialised condition in each case. In the case of the cross-vein system, there are no less than six evolutionary stages recognisable, which have been arranged in ascending order as A, B, C, D, E and F, with scores 1, $\frac{4}{5}$, $\frac{3}{5}$, $\frac{2}{5}$, $\frac{1}{5}$, and nil respectively (Section vii.).

In the case of fossil Orders, when the part of the wing showing a particular character has not been preserved, that character is shown in brackets in the condition in which it most probably existed in the fossil. It stands to reason that the missing characters, in the Permian and Triassic fossils, will almost certainly, when discovered, prove to have been present in the most archaic condition, A. The only exception made has been in the condition of the wing-coupling apparatus, which cannot be judged, and has therefore been entirely omitted.

The results obtained from the Table show that the two fossil Orders Paramecoptera and Protomecoptera are the most archaic, the Archetype of the latter scoring 90.0 per cent., and that of the former 86.1 per cent. Next to these comes the Archetype of the Mecoptera, with 77.8 per cent. The two Neuropteroid Orders, Megaloptera and Planipennia, have also very archaic Archetypes, with 73.9 and 65.6 per cent. respectively. The Paratrachoptera are the most specialised of the purely fossil Orders, with 66.5 per cent. The two Orders Trichoptera and Lepidoptera, as might be expected, come very close together, with 48.5 and 44.6 per cent. respectively. Finally, as was also very evident from the beginning, the most highly specialised Archetype is that of the Diptera, which possesses only 35.3 per cent of the total possible archaic characters.

The Phylogeny of the Orders of the Complex.

In Text-fig. 112, I have attempted to represent, by means of a Phylogenetic Diagram, the true relationships of the Orders comprised in the Complex, and their most probable lines of descent. All the known fossils have been made use of; and a series of small numerals are used as indicators for the positions

TABLE V.

TABLE OF THE CHARACTERS OF THE WINGS FOR THE ARCHETYPES OF THE COMPLEX AND ITS ORDERS.

| Ref. No. | Character | Complex | Mecoptera | Paramecoptera | Protomecoptera | Paratrichoptera | Diptera | Trichoptera | Lepidoptera | Megaloptera | Planipennia |
|---|---|---------|-----------|---------------|----------------|-----------------|---------|-------------|-------------|-------------|-------------|
| (1) | Tracheation of pupal wings:—A, Holo-tracheate. B, Merotracheate. | A | B | [A] | [A] | [B] | B | B | A | A | A |
| (2) | Costal Veinlets:—A, complete series. B, reduced to three. C, reduced to two. D, reduced to one only (<i>hm</i>). | A | A | B | A | A | D | C | C | A | A |
| (3) | Basal forking of Sc:—A, Sc' complete. B, Sc' reduced to a short vein. C, Sc reduced to veinlet <i>hm</i> . | A | C | C | A | B | C | C | C | C | C |
| (4) | Distal forkings of Sc and R ₁ :—A, present. B, Absent. | A | A | A | B | A | B | A | A | A | A |
| (5) | Manner of branching of Rs:—A, dichotomic. B, R ₂₊₃ pectinate. | A | A | A | A | A | A | A | A | B | B |
| (6) | Number of branches of Rs:—A, more than four. B, four only. | A | A | A | A | B | B | B | B | A | A |
| (7) | Number of branches of M ₁₋₄ :—A, more than four. B, four only. | A | A | A | A | B | B | B | B | B | B |
| (8) | Cubito-median Y-vein:—A, complete. B, reduced. | A | A | A | [A] | [A] | B | A | A | B | B |
| (9) | Distal fusion of M ₄ with Cu _{1a} :—A, absent. B, partial. C, complete. | A | A | A | B | A | A | A | C | A | A |
| (10) | Number of branches of Cu:—A, three. B, two. | A | B | A | A | B | B | A | A | A | A |
| (11) | Anal Y-vein in forewing:—A, absent. B, present. | A | A | A | A | A | A | B | B | A | A |
| (12) | Hindwing:—A, present. B, reduced to a halter. | A | A | A | A | A | B | A | A | A | A |
| (13) | Fusion of Cu ₂ with 1A near base in hindwing:—A, absent. B, present. | A | B | [A] | A | [A] | — | B | B | A | A |
| (14) | Marginal splitting or twigging of veins:—A, absent. B, present. | A | A | A | A | A | A | A | A | A | B |
| (15) | Cross-vein System:—A, quite unspecialised. B, C, D, E, F, consecutive steps in arrangement and reduction, ending with the most highly specialised (Dipterous) system. | A | A | C | B | B | F | D | E | B | B |
| (16) | Wing-trichiation; macrotrichia:—A, unspecialised, on main veins and archedictyon only. B, unspecialised, but absent from membrane. C, mostly specialised as scales. | A | A | A | A | A | A | A | C | A | B |
| (17) | Wing-trichiation; microtrichia:—A, normal. B, reduced. | A | A | [A] | A | [A] | A | B | B | A | A |
| (18) | Wing-coupling apparatus:—A, complete. B, jugal bristles lost. C, jugal bristles and frenulum both lost. | A | A | — | — | — | C | C | B | B | B |
| Comparative Archaism (percentage of archaic characters);— | | 100 | 77.8 | 86.1 | 90.0 | 66.5 | 35.3 | 48.5 | 44.6 | 73.9 | 65.6 |

Text-Fig. 112.

Phylogenetic Diagram for the Orders of the Panorpoidea Complex, as worked out on the characters of the wings only. The small numerals represent the geological and phylogenetic positions of the following important fossil types:—1, *Permochorista* (Upper Permian of Belmont, N.S.W.); 2, *Belmontia* (Upper Permian of Belmont, N.S.W.); 3, *Triadosialis* (Lower Trias of Germany); 4, *Mesochorista* (Upper Trias of Ipswich, Q.); 5, *Aristopsyche* and allied genera (Upper Trias of Ipswich, Q.); 6, *Archipanorpa* (Upper Trias of Ipswich, Q.); 7, *Archeopsyche* and *Protopsyche* (Upper Trias of Ipswich, Q.); 8, the *Palacontinidae* (Jurassic of England and Bavaria); 9, the *Kalligrammatidae* (Jurassic of Bavaria); 10, the Liassic Diptera; and 11, the *Necrotauliidae* (Lias of England and Germany). The vertical columns represent the consecutive geological ages, from Lower Permian up to Recent. The black lines showing the descent of the various Orders are made to vary somewhat according to the abundance of species in each Order at different geological horizons, and are shown as broken lines where the evidence is not sufficient to allow of a definite decision.

of the more important of these, in fixing the phylogenies of the various Orders. Where the line of descent of any given Order is shown as a continuous black line, this indicates that there is a reasonable amount of certainty that this line is correct. Where the line of descent is shown broken, then there is no reasonable certainty, either as regards the *character* of the ancestry, or as regards the *geological time* at which the Order began to evolve. The widths of the black lines, indicating the various lines of descent, are made to vary somewhat in proportion to the relative abundance in species of the Orders which they represent, at each geological period.

The following conclusions appear to be justified:—

The Archetype of the Complex, which may be defined as *that group of closely related forms from which all the Orders of the Complex arose*, must have existed in the Lower Permian, and possibly even in the Upper Carboniferous. As far as its wing-venation is concerned, it may have been a specialised offshoot from either the Palæodictyoptera or the Protorthoptera, both of which show closely similar types of wing-venation. It seems fairly certain that this Archetype is not represented by any known fossil, and it is probable that it arose in some part of the world far removed from any of the known insect-bearing beds of the Carboniferous.

The four Orders Mecoptera, Paramecoptera, Protomecoptera and Paratrachoptera represent a group of closely related forms, which will probably be included in a single enlarged Order Mecoptera when further discoveries in the Permian and Triassic Beds have been made. Every new type discovered from now on, belonging to this group of Orders, will manifestly tend to help to close up the gaps that at present exist between them. Consequently I have no hesitation in stating that *Mecopteroid forms* were the first Holometabolous Insects to appear, and that they were well represented, probably by all these four Orders, both in the Upper Permian and the Trias.

From the Table, it would appear that the Protomecoptera are, on the whole, the nearest to the Archetype of the Complex. This Order must clearly have existed alongside the Mecoptera and Paramecoptera in the Upper Permian, and serves in some measure to connect the two. Neither the Protomecoptera nor the Paramecoptera can be derived from the other; and we are compelled to assume that both arose from a common ancestral stem in the Permian. This common stem was evidently also the original main stem of the Panorpoïd Complex. From this main stem, apparently as a separate line of specialisation, in which Cu_1 became an unbranched vein, there arose the common stem of the true Mecoptera and the Paratrachoptera,—two very closely allied Orders, neither of which is derivable from the other, seeing that the Paratrachoptera possessed originally the basal branch of Sc , which the otherwise more archaic Mecoptera lacked. These relationships between the four Mecopteroid Orders are indicated by broken lines in the Phylogenetic Diagram (Text-fig. 112).

In the Upper Trias of Ipswich, the Paratrachoptera were well represented by some fine forms. These serve to connect the Mecoptera with the Diptera, and indicate very clearly the line of descent of this latter Order. While it is not claimed that any of the known types of Paratrachoptera from the Ipswich Beds are in themselves the *actual ancestors* of the Diptera, I think that there can be no doubt that some types within this fossil Order, by reduction of their hindwings and narrowing of the bases of their forewings, gave rise to the dominant Order Diptera of to-day. True Diptera first appear in the Lias; and these are, as might be expected, chiefly Nemocerous types, though a few show the condition of R_s typical of the Brachycera. The Cyclorrhapha probably arose in the Cretaceous, as

a side-branch from the older Brachycerous stem; their only known fossil representatives are of Tertiary age.

The line of ascent of the Paramecoptera leads directly to the common stem of the Trichoptera and Lepidoptera, as has been already shown in a previous paper (29). This common stem probably divided, somewhere in the Trias, into true Trichoptera, on the one hand, and Homoneurous Lepidoptera, of a Jugofrenata type, on the other. From this latter stem, the present Homoneurous Lepidoptera are directly derived. The *Micropterygidae*, *Eriocraniidae* and *Mnesarchaeidae* are three very reduced and isolated remnants of the original stem, the true Jugata a somewhat more successful side-branch, reaching a comparatively high stage of evolutions in the *Hepialidae*. The Jurassic *Palaeontinidae* may well have been a specialised offshoot from the old Homoneurous stem, unconnected in any way with present-day Heteroneurous types, seeing that the method of reduction of the veins of the hindwing is not the same in these fossils as it is in recent Heteroneura. The Heteroneura, representing, at the present day, the great bulk of the Order Lepidoptera, arose from the Homoneura as their archetypic family, the *Protocossidae*, probably either in the Upper Jurassic or in the Cretaceous; but the only known fossils definitely referable to this Suborder are of Tertiary age.

The two Neuropteroid Orders, Megaloptera and Planipennia, are venationally scarcely distinct enough to be retained separately, and are best regarded morphologically as two Suborders of a single Order Neuroptera. The Table shows that the common stem of these two Orders must have possessed a high percentage of archaic characters, and must have branched off from the original stem of the Complex very early. The recognition marks for fossil wings of these two Orders are the complete series of costal veinlets, and the pectinate form of Rs. The earliest known Megaloptera are found in the Lower Trias, the earliest Planipennia in the Upper Trias. But it is clear that the Archetype of the Megaloptera, at any rate, is more archaic than the Permian *Belmontia* in possessing a complete series of costal veinlets, and also in its type of cross-vein system. The possession of a distally forked Cu_1 marks the Megaloptera and Planipennia as an offshoot from the main stem of the Complex, rather than from the line of the true Mecoptera and the Paratrachoptera, which had this vein unbranched. Thus we are led

to indicate, by a broken line, a probable origin for these two Orders from the main stem of the Complex a little before the point represented by *Belmontia*. The earliest forms must obviously have been of Megalopterous appearance, the Planipennia being a specialisation from the very base of the old Corydalid stem.

The construction of a Phylogenetic Diagram has been undertaken in this Part, because the only available evidence, in the case of the Fossil Orders, is that of the venation. The lines of descent of the other Orders may have to be modified, when we have considered the evidence which a study of other parts may bring forward. But, on the other hand, that study will gain much in interest, now that we have the results founded upon the wing-venation set out clearly before us.

APPENDIX A.

Note on the Wing-Coupling Apparatus of the Micropterygidae (sens. lat.).

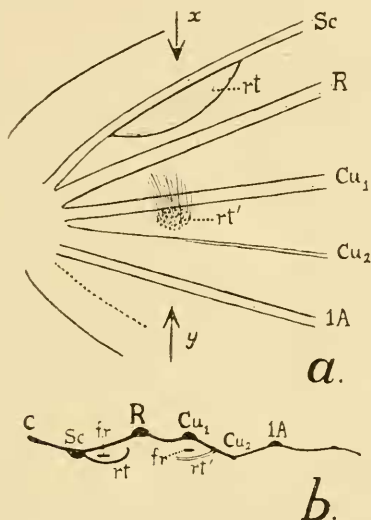
In a short paper in the Entomological News, (26), and also in Part i. of this work (24), I described the wing-coupling apparatus of this group of insects. I now call attention to a correction which I have made in this description, in my paper on these insects recently published (27). The original description of the jugal lobe is true for the *Micropterygidae* (sens. str.) and for the *Mnesarchaeidae*, but not for the *Eriocraniidae*, in which the jugal lobe is of the same type as in the Trichopterous *Rhyacophila*.

APPENDIX B. (Text-fig. 16, corrected).

Note on the occurrence of the retinacula in the Lepidoptera Heteroneura.

I am indebted to Dr. A. J. Turner, F.E.S., of Brisbane, for some valuable criticisms of the results contained in Part i. of this research, so far as they concern the structure of the retinacula in the Heteroneurous Lepidoptera. Dr. Turner points out that the male retinaculum, which I termed *radial*, is in reality *subcostal*. The error is mine, and I gladly accept the correction. He also points out that the female retinaculum does not actually spring from the cubitus, but from a position below it, and suggests that it be termed the *subdorsal* retinaculum. This is also correct, and the terminology which he suggests for the two

retinacula, *subcostal* and *subdorsal*, is an excellent one, which I gladly adopt. Consequently it will be necessary to alter the headings in the Table on p. 311 of Part i. (24), and to correct the lettering of Text-figs. 15-16 in that paper.



Text-Fig.16. (corrected).

- a*, Base of forewing of *Synemon* sp., male, from Killarney, Q., viewed from below, to show the correct positions of the two retinacula; *rt*, subcostal retinaculum; *rt'*, subdorsal retinaculum. ($\times 12$).
b, Section through same, taken along the line *xy* in fig. *a*, to show the positions of mechanical advantage of the two retinacula; *fr*, frenulum *in situ*. Other lettering as on p.535.

At the time Part i. was written, I had no fresh material of *Synemon*. Last summer Mr. E. J. Dumigan, of Clermont, Queensland, very kindly secured for me a number of fresh specimens of an undetermined species. I have descaled and cleared the wings of some of these, and give herewith a figure showing the exact positions of the two retinacula in the male (Text-fig. 16, *a*). It will be seen that the subdorsal retinaculum is a bunch of stiff hairs arising on the underside of the membrane, in the space between the strong convex vein *Cu* and the weak concave vein *Cu*₂, which is obsolescent in this genus.

It is evident that the retinacula, being developed upon the *underside* of the wing, will attain the most advantageous position if they are developed either on or near those veins which project most below the general level or plane of the wing-surface. The concave veins are Sc, M and Cu₂; of these, M has been eliminated during the formation of the basal cell. Text-fig. 16 *b*, shows diagrammatically the mechanical advantage of the positions in which the two retinacula actually occur.

Dr. Turner also points out that both subcostal and subdorsal retinacula occur commonly in the males of *Noctuidae*, *Arctiidae*, *Liparidae* and *Pyrallidae*, and can sometimes be detected in the *Geometridae*. He infers that "this double arrangement is the rule in the Heteroneura." Also, "in at least some female Noctuids there is an attempt at a subcostal retinaculum, though I cannot say that it is functional." He also draws my attention to the following interesting point:—"If you consult Sir G. Hampson's Catalogue of the Lepidoptera Phalænæ, vol. XI., you will find that the subfamily *Acontiinae* have normally a bar-shaped subcostal retinaculum in the male, but that, in some or all species of some genera, e.g. in *Earias*, this has been lost, and the frenulum articulates with the subdorsal retinaculum, as in the female. It is remarkable that, in two closely allied species, the male in one may have a well-developed subcostal bar-shaped retinaculum, in the other not."

There is, evidently, still a wide field of research open in the study of the evolution of the frenulum and its retinacula within the Lepidoptera Heteroneura.

APPENDIX C.

Note on the Resting-Position of the Wings in the Panorpoïd Complex.

During my research upon the Panorpoïd Complex, the Resting-Position of the Wings was carefully studied, with a view to giving a separate Part on this subject. The conclusions arrived at, however, show that no phylogenetic results of value can be attained, as regards the separate Orders. *All* the Orders of the Complex exhibit archaic types in which the resting-position is *stegopterous*, i.e. the wings are held, when at rest, in a slanting roof-like manner over the body. The angle of inclination of the wings depends, not only on their width, and the stoutness of the

build of the insect, but also upon the form of the resting-surface; as, for instance, in the case of the *Psychopsidae*, in which that angle is very acute when the insect rests upon a twig, and very obtuse when it rests upon a flat surface. In the more archaic Orders Mecoptera, Megaloptera and Planipennia, the stegopterous position of rest is practically universal. In the Trichoptera, it is the usual condition in all but the specialised *Hydroptilidae*. In the Lepidoptera, the stegopterous position is that adopted by all the Homoneura, and by many of the older forms within the Heteroneura. In the Diptera, the same position of rest is seen in the case of the *Psychodidae*, while the position of rest in the *Tabanidae* and many of the Cyclorrhapha (as in the Blowfly) shows little alteration from it.

The conclusion to be drawn from this is that, as regards the resting-position of the wings, the whole of the Complex was originally the same. The evidence, then, is in favour of a monophyletic origin for the Orders of the Complex, and helps to strengthen the conclusions already arrived at, from a study of the wing-coupling apparatus, the trichiation and the venation.

The stegopterous position of rest is found also in certain Orthoptera, and in the Psocoptera and the Homoptera. It is a more specialised position than the position with wings outspread (as in Anisopterous Odonata), or lifted vertically up over the body (as in Plecoptera), but more archaic than the flattened-down condition found in the Blattoidea, Perlaria (in which, also, the wings are more or less curved round the body), Heteroptera, Hymenoptera, etc.

BIBLIOGRAPHY.

(Note.—The reference numbers are made consecutive from Part to Part, but only those referred to in any given Part are printed with that Part).

2. HANDLIRSCH, A., 1908.—Die Fossilen Insekten. Leipzig, 1908.
3. MEYRICK, E., 1895.—“Handbook of British Lepidoptera.” London, Macmillan & Co., 1895.
5. TILLYARD, R. J., 1917.—“Mesozoic Insects of Queensland. No. 1. Planipennia, Trichoptera and the new Order Protomecoptera.” These Proceedings, 1917, xlii., Pt. i., pp.175-200.
6. ———— 1918.—“Permian and Triassic Insects from New South Wales in the Collection of Mr. John Mitchell.” *I.c.*, 1917, xlii., Pt. iv., pp.720-756.
9. MEYRICK, E., 1917.—“Descriptions of South African Lepidoptera.” *Ann. S. African Mus.*, 1917, xvii., Pt. i., No. 1, pp.17-19. (*Prototheoridae*, pp.17-19).
12. TILLYARD, R. J., 1916.—“Studies in Australian Neuroptera.” No. iv. *I.c.*, 1916, xli., Pt. ii., pp.269-332.

13. ———— 1917.—“The Wing-Venation of Lepidoptera.” (Preliminary Report), *l.c.*, 1917, xlii., Pt. i., pp.167-174.
14. COMSTOCK, J. H., and NEEDHAM, J. G., 1898.—“The Wings of Insects.” *American Naturalist*, 1898-9, xxxii.-xxxiii. (*Sthenopsis*, 1899, xxxiii., p.253).
15. COMSTOCK, J. H., 1918.—“The Wings of Insects.” Comstock Publishing Co., Ithaca, N.Y., 1918.
16. MACGILLIVRAY, A. D., 1912.—“The Pupal Wings of *Hepialus thule*.” *Ann. Ent. Soc. Amer.*, 1912, v., pp.239-245.
17. MEYRICK, E., 1916.—“Note on Some Fossil Insects.” *Ent. Mo. Mag.*, 3rd Ser., No. 20 (No. 627), Aug. 1916, pp.180-182.
18. TILLYARD, R. J., 1914.—“On Some Problems concerning the Development of the Wing-Venation of Odonata.” *These Proceedings*, 1914, xxxix., Pt. i., pp.163-216. (See p.206).
19. ———— 1915.—“On the Development of the Wing-Venation in Zygopterous Dragonflies, with Special Reference to the *Calopterygidae*.” *l.c.*, 1915, xl., Pt. ii., pp.212-230. (See p.224).
20. ———— 1916.—“Mesozoic and Tertiary Insects of Queensland and New South Wales.” *Qu. Geol. Surv.*, Publ. No. 253, 1916, pp.1-47. (*Mesochorista*, p.29, Pl. 2, fig.2).
21. ———— 1917.—“The Biology of Dragonflies.” Cambridge Univ. Press, 1917.
22. ———— 1918.—“Mesozoic Insects of Queensland. No. 2. The Fossil Dragonfly *Aeschnidiopsis flindersiensis* (Woodward), from the Rolling Downs (Cretaceous) Series.” *These Proceedings*, 1917, xlii., Pt. iv., pp.676-692.
23. ———— 1918.—“Studies in Australian Mecoptera, No. ii. The Wing-Venation of *Chorista australis* Klug.” *l.c.*, 1918, xliii., Pt. ii., pp.395-408.
24. ———— 1918.—“The Panorpoïd Complex. Part 1. The Wing-Coupling Apparatus, with Special Reference to the Lepidoptera.” *l.c.*, 1918, xliii., Pt. ii., pp.286-319.
25. ———— 1918.—“The Panorpoïd Complex. Part 2. The Wing-Trichiation, and its Relationship to the General Scheme of Venation.” *l.c.*, 1918, xliii., Pt. iii., pp.626-657.
26. TILLYARD, R. J., 1918.—“*Micropterygidae* not of the Jugate Type.” *Ent. News*, xxix., March, 1918, p.99.
27. ———— 1919.—“On the Morphology and Systematic Position of the Family *Micropterygidae* (sens. lat.).” *Introduction and Part i. The Wings.* *These Proceedings*, 1919, xlv., Pt. i., pp.95-136., Pl. iii.
28. ———— 1919.—“Mesozoic Insects of Queensland. No. 5. Mecoptera, the new Order Paratrachoptera, and additions to the Planipennia.” *l.c.*, 1919, xlv., Pt. i., pp.194-212.
29. ———— 1919.—“A Fossil Insect-wing belonging to the new Order *Paramecoptera*, ancestral to the *Trichoptera* and *Lepidoptera*, from the Upper Coal-Measures of Newcastle, N.S.W.” *l.c.*, 1919, xlv., Pt. ii., pp.231-256.
30. ———— 1919.—“Studies in Australian Neuroptera. No. 8. The Family *Ithonidae*.” *l.c.*, 1919, xlv., Pt. ii., pp.414-437.

31. TURNER, A. J., 1916.—“A new Micropterygid from Australia.”
Trans. Ent. Soc. London, Parts iii., iv., June, 1916, pp.391-393.
32. ——— 1918.—“Observations on the Lepidopterous Family
Cossidae and on the Classification of the Lepidoptera.” *l.c.*,
1918, Parts i., ii., No. ix., pp.155-190.
33. ULMER, G., 1907. — “Trichoptera” in “Genera Insectorum,”
Vol. ix., Fasc. 60, pp.1-259, Pls. 1-41. Brussels, M. P. Wyts-
man, 1907.
34. WEELE, H. W. van der, 1910.— “Megaloptera, Monographic Re-
vision” in Coll. Zool. du Baron E. de Selys-Longchamps.
Fasc. v. Brussels, 1910.

EXPLANATION OF PLATES.

Plate xxxi.

(Order PARAMECOPTERA).

- Fig. 15. *Belmontia mitchelli* forewing (x 19); basal portion to show
the cubito-median Y-vein.
- Fig. 16. Portion of same wing, further enlarged (x 42½), to show the
trichiation of M₅ and Cu₁. (The arrows point to the bases of
two macrotrichia, one on M₅, and the other on Cu₁.)

(This Plate is the same as Plate xiii. in the paper numbered (29)
in the Bibliography).

Plate xxxii.

(Order LEPIDOPTERA).

- Fig. 17. *Charagia splendens* Scott (fam. *Hepialidae*). Base of pupal
forewing (x 18). To show the formation of M from two sepa-
rate tracheæ, one from the costo-radial and the other from
the cubito-anal group. (The edge of a cover-slip is visible
crossing the tracheæ near their bases).
- Fig. 18. *Charagia eximia* Scott (fam. *Hepialidae*). Base of pupal
forewing (x 56), from a specimen in which M and Cu arise
close together from the cubito-anal group. Base of wing to
the right; above, a portion of R, showing multiple origin.

Plate xxxiii.

(Order LEPIDOPTERA).

- Fig. 19. *Nyleutes eucalypti* Scott (fam. *Cossidae*). Base of pupal
forewing (x 10), to show the formation of the anal Y-vein by
shortening of 2A. 3A is marginal.
- Fig. 20. *Charagia eximia* Scott (fam. *Hepialidae*). Base of pupal
hindwing (x 19), to show the union of Cu₂ with 1A near the
base, and their separation further distad.

Plate xxxiv.

(Order LEPIDOPTERA).

- Fig. 21. *Wingia lambertiella* Wing. (fam. *Oecophoridae*). Middle
portion of pupal forewing (x 20), to show the five-branched R,
the three-branched M and Cu, and portion of 1A. (The origin
of Cu₂ lies to the right, just outside the photograph).
- Fig. 22. *Carpocapsa pomonella* (Linn.) (Superfam. Tortricina).
Basal portion of pupal forewing (x 57), to show cubital fork
and formation of anal Y-vein.

Plate xxxv.

(Order LEPIDOPTERA).

- Fig. 23. *Xyleutes eucalypti* (Scott) (fam. *Cossidae*). Lower distal portion of pupal forewing, to show the branches of M (in middle) and Cu₁, (x 6). A small part of Cu₂ is seen in the lower right-hand corner.
- Fig. 24. Small part of hindwing of same pupa, much enlarged (x 10), to show the fusion of Sc (the large upper trachea) with R₁. Note also the simple Rs. Base of wing lies to the right, and a part of M is visible in the lower portion of the photograph.

Postscript, added 30th September, 1919:—During a recent visit to Jervis Bay, I carried out some researches which have strengthened certain conclusions come to in this paper. These may be briefly summarised as follows:—

(1) A native Cockroach of the genus *Escala* was found very commonly under bark, and a number of specimens were taken which were still white and soft after undergoing an ecdysis. The wing-sheaths of these were dissected off, and the tracheation carefully studied. The result is that there can be no doubt whatever that the *vena dividens*, determined by Comstock as vein 1A fused with Cu, is in reality vein Cu₂. Thus the Cockroaches fall into line with the insects of the Panorpoïd Complex, as well as with the Cicada and the Psocids, already mentioned in Section iv. of this paper.

(2) Further research upon the wing-tracheation of the *Hesperiidae* was carried out by obtaining pupæ of the well-known Skipper, *Hesperilla picta* Leach, in fine condition, and dissecting out their wings. This insect belongs to the Subfamily *Trapezitinae*. The results show that its pupal tracheation agrees in every important particular with that of *Euschemon rafflesia* already dealt with fully in this paper (Section xiv.). The only important difference is to be found in the imaginal venation, the vein M₂ failing to chitinise in the hindwing of *H. picta*, whereas it does so in the hindwing of *E. rafflesia*. We may therefore conclude from this, (a) that *Euschemon* is a true Hesperiid, and (b) that the Butterflies as a whole are a monophyletic group, the first dichotomy of which resulted in two lines of evolution, one leading to the *Hesperiidae*, with *Euschemon* as an archaic offshoot from near its base, and the other leading to all the rest of the Butterflies. It is clear that no existing type of Hesperiid represents the ancestral type of the Butterflies; but, on the other hand, *Euschemon* itself has not departed far from that lost ancestral type. R. J. T.